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5. Middle Ordovician Ostracodes of Central and Southern Sweden

By

Valdar Jaanusson

ABSTRACT.—The paper gives a description of the palaeocope ostracodes from the *Platyurus*, *Schroeteri*, *Crassicauda*, and *Ludibundus* beds of central and southern Sweden. The sequence of strata examined corresponds to the uppermost Llanvirnian, Llandeilian, and the lowermost Caradocian of the modern classification of the British Ordovician. The terminology of the palaeocope carapace is revised, and several new terms are proposed. A brief account is given of the formation of lobes and ornamental extensions. The dimorphism of certain palaeocopes is discussed in some detail. Four different types of dimorphism are distinguished, termed kloedenellid, cruminal, velar, and histial, each characterizing a separate superfamily. The locular dimorphism is regarded as a special type of the histial dimorphism. The suborder *Palaeocopa* is divided into seven superfamilies: *Eurychilinacea*, *Hollinacea*, *Beyrichiacea*, *Kloedenellacea*, *Kirkbyacea*, *Leperditellacea*, and *Leperditiacea*. The classification of eurychilinaceans, hollinaceans, and leperditellaceans is treated in detail. The following new family-group taxa are proposed: *Chilobolbininae* nov. and *Oepikellinae* nov. within *Eurychilinidae*, *Tvaerenellinae* nov. within *Piretellidae*, and *Oepikiumidae* nov. within *Hollinacea*. Fourteen new generic names are proposed. Altogether 62 species are described, including 23 new species and 10 species which are evidently new, but which cannot be defined at present. The erection of new species of dimorphic genera when one of the dimorphs is unknown is discouraged. Specimens of 10 additional species, mostly types or topotype material, are figured. Apart from the new specific names listed in the contents *Tallinnella? hloubetinensis* n.sp. and *Sigmobolbina monoceratina* n.nom. are introduced.

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Introduction

This paper forms a part of the present writer's studies on the Middle Ordovician of Sweden, and is intended as a study of the ostracode fauna of the uppermost Lower Ordovician and the lower and middle parts of the Middle Ordovician of Central and Southern Sweden. The stratigraphic succession of the rocks from which the palaeocope ostracodes are described is as follows (the correlation of the shelly and the graptolitic successions chiefly after JAANUSSON & STRACHAN 1954):

Ludibundus beds	Zone of *Nemagr. gracilis*
Crassicauda beds	Subz. of *Climacogr. haddingi*
Schroeteri beds	Subz. of *Glossogr. hincksi*
Platyurus beds	Zone of *Didymogr. murchisoni*

The subzones of *Climacograptus haddingi* and of *Glossograptus hincksi* were considered by JAANUSSON & STRACHAN as a single zone corresponding to the zone of *Glyptograptus teretiusculus* of the British classification of the graptolitic succession. Following JAANUSSON & STRACHAN (1954; cf. also JAANUSSON 1953, p. 461) the boundary between the Lower and Middle Ordovician is placed between the zones of *Didymogr. murchisoni* and *Glyptogr. teretiusculus* in the graptolitic, and between the *Platyurus* and the *Schroeteri* beds in the shelly succession, i.e. between Llanvirn and Llandeilo as defined in the modern classification of the British Ordovician.

The stratigraphic terminology of the shelly facies of the Swedish Lower and Middle Ordovician is at present in some state of confusion. The different divisions of the shelly facies listed above represent time-rock units of the stage category. According to the practice common for the Swedish Cambrian and Ordovician these units are, however, named after a species and not after a locality as in most other countries. Moreover, the specific names are used usually together with the names of the rock, as "limestone" or "mudstone". As, however, the lithological variation of the rock within each division is rather considerable, different names of rocks, or the more neutral term "beds", may be used for the same division in different districts. This practice is provisionally followed also in the present paper. The stratigraphic terminology of the Swedish Middle Ordovician will be treated in a future paper.

For purely practical reasons the upper limit of the beds examined is drawn not at the boundary between the *Ludibundus* and *Macrourus* beds, but at the beginning of the complex of bentonite beds in the uppermost *Ludibundus* limestone. As to Västergötland the ostracodes from beds beneath the *Schroeteri* mudstone are not described here, it appearing more advisable to treat them together with the ostracodes of the upper part of the *Vaginatum* limestone.

The stratigraphy and lithology of the beds containing the ostracode fauna described in the present paper will be treated in a series of coming papers on

the Middle Ordovician of Central and Southern Sweden (excl. Scania). There also a detailed stratigraphical distribution of the ostracode species will be given together with a discussion on their palaeoecology.

Historical Survey

The ostracodes from the *Ludibundus* limestone and corresponding beds in Sweden have been treated already by several authors, in the first place by THORSLUND (1940, 1948). Some ostracodes have been recorded also from the *Crassicauda* limestone.

LINNARSSON (1869a, b) described *Beyrichia* (= *Steusloffia*) *costata* LINNARS. from Västergötland, and called (1869b), in view of the occasionally abundant occurrence of this species, a part of the Ordovician sequence in this district the *Beyrichia* limestone (= the middle and upper part of the *Ludibundus* beds). KOLMODIN (1869) described *Beyrichia bilobata* KOLM. [= internal mould of *Steusloffia* cf. *costata* (LINNARS.)] from regio C (= *Ludibundus* beds) of Ålleberg, Västergötland. TÖRNQUIST (1883, p. 19) recorded *Beyrichia costata* LINNARS. [= *Steusloffia linnarssoni* (KRAUSE) + *Tallinnella dimorpha* ÖPIK according to his collections in the Museum of the Palaeont. Inst. of Lund] from the Flagkalk (= *Crassicauda* limestone) of the Siljan district. HADDING (1913) described *Primitia Tolli* BONNEMA [= *Conchoprimitia*? *conchoidea* (HADDING)], *Primitia* (= *Conchoprimitia*?) *conchoidea* HADDING, and *Primitia* (= *Pyxion*) *carinata* HADDING from the *Nemagraptus gracilis* beds of Scania. The ostracode faunas from the Lower *Chasmops* (= *Ludibundus*) limestone of the Brunflo-Lockne area, Jämtland, and the erratic boulders of the Tvären area, Södermanland, were comprehensively treated by THORSLUND (1940). He recorded (pp. 186–187) from these beds 33 different species, 15 of which were new and others identified with species previously described from Estonia or the North German erratic boulders. Eight of these species were merely listed, the others described and illustrated. Two new genera, viz. *Balticella* and *Öpikella* (= *Oepikella*, cf. p. 217), were erected. JAANUSSON (1947, p. 46) listed *Tallinnella dimorpha* ÖPIK and *Steusloffia* aff. *costata* (LINNARS.) [= *S. linnarssoni* (KRAUSE)] from the *Crassicauda* limestone of the Siljan district. THORSLUND (1948) described the ostracode fauna from the Kullatorp bore, Kinnekulle, Västergötland, including 6 new species from the beds corresponding to the *Ludibundus* limestone, and gave a redescription of *Pyxion carinatus* (HADDING) and *Steusloffia costata* (LINNARS.). Seven additional species were listed in the text. From the lowermost layers of the core (below 84.90 m), corresponding to the uppermost *Crassicauda* and the lowermost *Ludibundus* beds (cf. JAANUSSON & STRACHAN 1954, p. 687), THORSLUND (1948, p. 350) recorded the following species: *Euprimitia* cf. *locknensis* [= *Euprimites locknensis* (THORSL.)], *Conchoprimitia* cf. *tolli integra* ÖPIK (= *C.* cf. *leperditioidea* THORSL.), *Winchellatia* aff. *variolaris* (= *Sigmobolbina* cf. *sigmoidea* n. sp.), *Bromidella coelodesma* (ÖPIK) (= *Uhakiella* cf. *coelodesma*), *Chilobolbina dimorpha* THORSL. [= *Laccochilina* (*Laccochilina*) sp. indet.], *Steusloffia* aff. *costata* [= *S. costata* (LINNARS.) + *S. multimarginata* ÖPIK + *S.* sp. indet.], and *Tallinnella dimorpha* ÖPIK. Also from the uppermost part of the Norra Skagen core, Kinnekulle, from the beds corresponding to the lower part of the *Ludibundus* and the uppermost *Crassicauda* beds, some ostracode species were listed by THORSLUND (1948, pp. 359–360), *viz. Primitia* (= *Parapyxion*) *subovata* THORSL., *Bromidella coelodesma* (ÖPIK) (= *Uhakiella* cf. *coelodesma*), *Tallinnella dimorpha* ÖPIK, *Chilobolbina dimorpha* THORSL. [= *Laccochilina* (*Laccochilina*) sp. indet.], *Steusloffia* aff. *costata* (LINNARS.) [= *S. linnarssoni* (KRAUSE) + *S. multimarginata* ÖPIK + *S. costata* (LINNARS.)], *Ceratopsis* aff. *perpunctata prominens* ÖPIK (= *Sigmoopsis bergsbrunnae* n. sp.), and *Ctenentoma* cf. *polytropis* (ÖPIK) (= *Oecematobolbina* sp.). HEDE (1951) listed *Conchoprimitia conchoides* (HADDING) and "*Primitia*" *tolli* HADDING (= *Conchoprimitia*? *conchoidea*) from

the *Nemagraptus gracilis* beds of a boring in the Fågelsång district, Scania, and NILSSON (1951) *Conchoprimitia* sp. (= gen. et sp. indet.) from the beds with *Trinucleus bronni* of SE. Scania. LINDSTRÖM (1953) described from the Sularp shale (= upper part of the *Ludibundus* beds) of the Fågelsång district, Scania, *Primitiella? spiniger* LINDST., and listed some other species including *Eurychilina suecica* THORSL. (= *Actinochilina* cf. *suecica*) and "*Primitia*" *tolli* HADDING [= *Conchoprimitia*? *conchoidea* (HADDING)]. JAANUSSON (1953) reported *Chilobolbina dentifera* (BONN.) (= *C.* aff. *dentifera*) from an erratic boulder of the South Bothnian area. Some other occasional reports also exist of ostracodes from the sequence of the strata concerned, but the vagueness of the determinations prevents as a rule the recognition of the species.

The above review proves that some information has been available on the palaeocope ostracodes from the *Crassicauda* beds of the Siljan district and Kinnekulle, and also a rather comprehensive knowledge of those from the *Ludibundus* limestone and corresponding beds of the Autochthonous of Jämtland, the Tväre area (Södermanland), Kinnekulle (Västergötland), and Scania. The ostracode faunas from the *Platyurus* and *Schroeteri* beds were, however, as yet completely unknown.

From the papers by BONNEMA (1909) and ÖPIK (1937) the ostracodes are well known from the Uhaku and Kukruse Stages of Estonia, these stages corresponding to the *Crassicauda* and the lower part of the *Ludibundus* beds, respectively. The stratigraphic distribution of the ostracodes in the Middle Ordovician of Estonia has been recently summarized by SARV (1956a). The rather poor ostracode fauna of the corresponding beds of the Oslo region, Norway, has been described by HENNINGSMOEN (1953b).

The Material Studied

The following abbreviations are used to indicate the whereabouts of particular specimens or material:

LM Museum of the Palaeontological Institute, Univ. of Lund.
OM Palaeontological Museum, Oslo.
RM Palaeozoological Department, State Museum of Natural History, Stockholm (Naturhistoriska Riksmuseet).
SGU Museum of the Geological Survey of Sweden, Stockholm (Sveriges Geologiska Undersökning).
SH Geological Institute, Univ. of Stockholm.
SMC Sedgwick Museum, Univ. of Cambridge.
TM Geological Museum, Academy of Science, Tartu.
UM Museum of the Palaeontological Institute, Univ. of Uppsala.

The assembling of the material described in this paper began already in 1945, when Drs. JÜRI MARTNA, HINREK NEUHAUS, and the present writer secured a series of samples from the *Crassicauda* limestone of Furudal and Fjäcka, Siljan district, to be examined for ostracodes. Also several samples from marly layers intercalated between the limestone beds were collected in hope of washing out ostracodes in the way we were used to when working in the Estonian sequence of strata. The result was, however, rather disappointing as the rocks in the Siljan district appeared to be too much pressed tectonically. In the same year also a large South Bothnian erratic boulder (= Bergsbrunna

boulder No. 1) of uppermost *Crassicauda* limestone was found (UM). In the following years the present writer was occupied on different occasions with searching for and extracting the ostracodes in this interesting boulder. In 1947 he was engaged in the search for fossils, mostly ostracodes, from the parts of the Norra Skagen bore, Kinnekulle, corresponding to the *Schroeteri* and *Crassicauda* beds. This was done in connection with an investigation planned by Prof. P. THORSLUND, then at the Geological Survey of Sweden. The need for a comprehensive treatment of the ostracodes from the sequence of the strata studied made itself felt when the present writer was assigned the description of the *Platyurus* limestone and the Middle Ordovician of the Böda Hamn bore, Öland, and later of the corresponding parts of the Gammalsby and Skärlöv bores on Southern Öland. On account of the scarcity of macrofossils in most parts of the cores it was impossible to carry out a detailed stratigraphical subdivision of the core sections without the help of the often rather abundantly occurring ostracodes. These studies have resulted in the present paper.

On a future occasion a detailed account will be given of the localities, and the bores from which the greatest part of the material of ostracodes described in this paper is derived. Altogether the following material has been examined: (1) Siljan district, Dalarna. Stratigraphically precisely determined series of limestone samples from 8 localities, collected chiefly from sections exposed by excavations in 1946–1948 (UM). (2) Erratic boulders from the South Bothnian area. Only 3 boulders (UM), which contained an assemblage of macrofossils sufficiently indicative of the exact stratigraphical horizon, were subjected to a detailed examination. (3) Erratic boulders from the Tväre area, Södermanland. In addition to the material studied and described by THORSLUND (1940) new boulders collected from this area by Prof. P. THORSLUND, Dr. T. TJERNVIK, and the present writer in 1954 (UM). (4) Öland. Cores from the Böda Hamn (UM), Gammalsby (SGU), and Skärlöv (SGU) borings, and series of limestone samples from different representative localities (UM). A collection of ostracodes from different localities collected by J. G. ANDERSSON (RM). (5) Östergötland. Cores from the Motala and Smedsby Gård borings (SGU). (6) Västergötland. All material of the Kullatorp boring (UM), studied and described by THORSLUND (1948). Cores from the Norra Skagen and Stora Åsbotorp borings (SGU). (7) Scania. Material described by HADDING (1913) and additional specimens collected by M. LINDSTRÖM (LM).

The well-preserved ostracodes from the *Ludibundus* limestone from the Autochthonous of Jämtland, northern Sweden, collected and described by THORSLUND (1940) (SGU) have been used mainly for comparative purposes. Material of the species occurring both in this area and in central and southern Sweden has been included in the description of the respective species; one additional, taxonomically and morphologically interesting species, *Lomatobolbina mammillata* (THORSLUND), unknown so far outside this area, is treated here.

Of the species previously described by THORSLUND (1940, 1948) from the *Ludibundus* beds not all are redescribed. Of some species, viz. *Levisulculus* (?) *reticulatus* (THORSL.), *Ulrichia* (?) *reticulata* THORSL., *Winchellatia* (= *Lomatobolbina*?) *gunnari* THORSL., and *Pyxion kinnekullensis* THORSL. no material beyond that studied and described by THORSLUND has been found, and the reader is referred to the original descriptions and illustrations. Of most of these species only one or two specimens are known. *Balticella oblonga* THORSLUND is not considered as no important additions can at present be made to the description by THORSLUND (1940, p. 180). Of *Primitia*? (= *Levisulculus*) *extraria* ÖPIK, listed by THORSLUND (1940, p. 186) from the Tvären area, no specimen has been found in the collections, and the occurrence of this species in Sweden needs further confirmation.

The material of *Palaeocopa* examined from the sequence of strata studied includes, in addition to the species described in the present paper, also specimens of at least 9 additional species, probably all new, and three of them obviously belonging to new genera. The present material of these species, however, does not suffice for a characterization of the species.

For purposes of comparison the present writer succeeded in obtaining, from samples of the rocks from the Kukruse Stage, Estonia, belonging to UM, RM, and OM, a great number of the species described by BONNEMA (1909) and ÖPIK (1937). Some of these specimens already extracted by Dr. HENNINGSMOEN from the rock samples belonging to OM, were kindly turned over to the present writer. Also some specimens from the Kukruse Stage of Estonia are figured here. This material has been of great importance for the present study as the ostracode faunas of the Kukruse Stage include species very similar to, or identical with, those of the *Ludibundus* beds of Sweden, and also since the good preservation of the Estonian material made it especially suitable for comparative morphological investigations. Unfortunately no material from the Uhaku Stage of Estonia was available for comparison. This has caused some uncertainty in the identifications of the possibly identical or nearly related species from Sweden [cf. e.g. *Euprimites* cf. *eutropis* (ÖPIK), *Uhakiella* cf. *coelodesma* ÖPIK]. In a rock sample from the *Lepidurus* limestone ($B_{II}\gamma$) of Tallinn, Estonia (UM), the present writer was, furthermore, able to find several ostracodes described by ÖPIK (1935), including the type species *Rigidella mitis* (ÖPIK), *Laccochilina* (*Laccochilina*) *estonula* (ÖPIK), and *Conchoprimitia gammae* ÖPIK. Also one of these specimens is figured in the present paper. Thanks to Dr. HENNINGSMOEN's kindness the present writer was able to examine practically all the material from the Lower and Middle Ordovician of the Oslo region described by him 1953b and 1954a. Some of his original specimens are refigured here.

During the examination of the material many morphological and taxonomical questions arose. For dealing with them a considerably greater first-hand knowledge of the palaeocope ostracodes was needed than offered by the material

mentioned above. For these purposes much material outside the sequence of the strata studied was examined. Great use was made of the large collection of Lower Ordovician ostracodes from the Siljan district, Sweden, collected and described by HESSLAND (1949) (UM), of the Upper Ordovician material from the Kullatorp core described by HENNINGSMOEN (1948) (UM), and of the fine collection of ostracodes from the erratic boulders of the uppermost Middle Ordovician *Macrourus* calcareous siltstone from Öland collected and studied by J. G. ANDERSSON (1893) (RM). At the time when Prof. J. G. ANDERSSON was working on the Swedish Ordovician ostracodes in the nineties of the last century, a work of which unfortunately only some brief summaries were ever published, Dr. E. O. ULRICH sent a collection of North American Ordovician ostracodes to the RM for comparison. This valuable collection, including "*Leperditella*" *tumida* (ULRICH), *Drepanella ampla* ULRICH, 1890, and several species of *Ctenobolbina*, *Ceratopsis*, and *Bollia*, was kindly put at the present writer's disposal by the authorities of the RM. Further material borrowed from the same museum included a collection of Bohemian Ordovician ostracodes, obviously determined by J. BARRANDE, and containing among others numerous topotype specimens of *Tallinnella? bohemica* (BARR.) and *Parapyxion prunella* (BARR.). During a stay in the autumn of 1955 at the Senckenberg Museum, Frankfurt a.M., the writer had the opportunity of examining the type specimens and other material described by E. A. SCHMIDT (1941) from the Bohdalec beds of Bohemia. This examination has led to the erection of the new species *Tallinnella? hloubetinensis* in the present paper.

The author also enjoyed the possibility of examining Ordovician ostracodes from U.S.A., obtained through and partly collected by Prof. I. HESSLAND (UM, OM, SH). Dr. R. V. KESLING kindly sent a sample containing numerous specimens of *Quadrijugator permarginatus* (FOERSTE) from the Ordovician of Michigan. Through the courtesy of Prof. I. HESSLAND the present writer obtained numerous washed samples with Devonian ostracodes presented by Dr. R. V. KESLING from several localities described by him. Of these samples especially that from the Arkona shale, Ontario (cf. KESLING 1953a) contained numerous well-preserved hollinids, including *Ctenoloculina* and *Falsipollex* (SH). These samples provided the opportunity of obtaining a first-hand knowledge of the morphology of the Devonian hollinids.

Without access to all this material a comprehensive discussion on the taxonomy and morphology of the palaeocope ostracodes would scarcely have been possible.

Methods of Study

A general account of the methods of study of ostracodes in a state of preservation similar to that of the material treated here is given by HESSLAND (1949, pp. 114–118), and most of his considerations are not repeated here.

The material described consists mainly of separate valves embedded in the rock. Only a comparatively small number of free carapaces could be obtained. The state of preservation is rather variable. Specimens from the Tvären area are as a rule excellently preserved, as is occasionally also some material from other districts. On the ostracodes from argillaceous limestone dissolution of the protruding parts of the shell often effaces the details of ornamentation, and amongst those from mudstones a large percentage is too badly preserved to allow of specific determination.

The rock samples as well as one half of the drilling cores were crushed, and the fragments of rock of somewhat varying size were subjected to a close search under a magnification of × 20. The cores of the borings of Smedsby Gård, Motala, and Stora Åsbotorp were examined for ostracodes by Mrs. Meit Lindell, without whose valuable and skilful help the present study could not have been finished for several years to come.

The ostracodes found were cleaned by the present writer with fine needles, and the preparation of the material for description and measurement has been very laborious. Great care was exerted to expose the subvelar or subhistial fields, but often with only scant success. In several cases the hard and often rather brittle rock did not allow the complete preparation of the rather tiny ornamental extensions, and for some species the information about the exact shape and position of the adventral structures had unfortunately to remain rather incomplete. Specimens which were preserved well enough to allow of specific determination were studied in their ordinary state as well as with a thin coating of ammonium chloride, and also immersed in alcohol or some oil. The ammonium chloride coating was used for revealing of details of the ornamentation, immersion in different fluids mainly for the detection of possible traces of muscle scars, and also for the examination of the internal structure (cf. also Hessland 1949, pp. 116–117).

For photographing a Leitz *Panphot* was used. The photographs were taken on Gevaert Replica photographic plates (23°). For prints dessigned for collotype plates Kodak mat Kodura paper, and for those intended for half-tone plates Gevaert blanc Ridax paper was used. Unfortunately the supply of the former paper was limited, and as this brand does not seem to be manufactured any more, some difficulties arose in getting satisfactory prints for the two last collotype plates. The magnification as stated in the explanation of the plates is not entirely exact, as due to the rather great convexity of most specimens small differences in the size of the outline from the scale given are unavoidable. Most specimens photographed were whitened with an ammonium chloride coating; only some photographs were taken without this coating, or while immersed in alcohol. Great care must be taken to free the specimens from all traces of fat before applying the coating of ammonium chloride (cf. also Hessland 1949, p. 116). For this reason the specimens must be washed carefully in alcohol beforehand.

Sufficiently good photographs were obtained only after many tedious experiments. All photographic work was most skilfully carried out by Mr. N. HJORTH, the photographer of the Palaeontological Institute of Uppsala. Most photographs were only slightly retouched by Mr. E. STÅHL. The text-figures of the different species were drawn for the most part directly after enlarged prints by Mr. E. STÅHL and Mrs. I. THOMASSON.

Measurements

Practically all non-compressed specimens with undamaged outline were measured with a Wentworth-Hunt integrating stage. The accuracy of the reading was 0.005 mm. Of several species a large number of specimens has been examined, but most of them were usually too incomplete in some way or other to allow exact measuring; thus the actual number of measured specimens compared with those examined was, with some exceptions, rather small. This was especially the case with species of small size or young instars which were generally less perfectly preserved or also more easily damaged by preparation. At measuring the specimen was fixed to a lump of plasticine, and great care was taken to give the specimen the correct orientation. With small specimens a slight change in the angle at which the valve is viewed will cause a rather considerable variation in the readings. The exact orientation of specimens embedded in matrix is also usually more difficult than that of loose valves or carapaces. All measurements were, therefore, repeated twice or more, depending on the amount of the difference in the readings, and in the tables the average of different readings is given. Before each new reading the specimen was removed from the plasticine, and the orientating repeated. In spite of all these precautions the accuracy of the dimensions of the specimens still embedded in the rock is apparently inferior to that of the freed specimens. This is due mainly to the often experienced difficulty of determining the outlines of the specimen against the surrounding rock with sufficient distinction.

On all specimens length and height were measured, in most cases in the usual sense of these terms, i.e. including the ornamental extensions. However, on account of the very variable development and preservation of the latter different definitions, which are stated from case to case, had sometimes to be applied to these terms. Thus, for practical reasons in addition to, or instead of, the length and height of the valve also length and height of the domicilium, or those of the lateral surface of the domicilium, were occasionally measured. The width of the valve was not measured as the difficulties to give the specimen the exact orientation proved too great and, consequently, the different readings showed too large divergences to be of practical use. Also in many specimens the free edge could not be exposed. The length of the hinge-line was measured in all species with sufficiently distinct cardinal corners. In *Euprimites* the length

of the sulcus was measured in addition. All measurements were carried out by the present writer.

The following abbreviations have been used in the tables of dimensions:

L. valve Greatest length of the valve, the marginal structures being excluded.
H. valve Greatest height of the valve, the marginal structures being excluded.
L. domic. Greatest length of the lateral surface of the domicilium.
H. domic. Greatest height of the lateral surface of the domicilium.
L. lob. Greatest length of the lobate area.
H. lob. Greatest height of the lobate area.
H-L Length of the hinge-line, i.e. the distance between the cardinal corners.
L. sulcus Length of the sulcus, i.e. the distance between the ventral end of the sulcus and the dorsal margin of the valve.

c carapace.
h heteromorph.
l left valve.
r right valve.
t tecnomorph.

All dimensions are given in mm.

Acknowledgements

For the first introduction to the Middle Ordovician ostracodes the writer tenders his sincere gratitude to his teacher Prof. A. Öpik (formerly at the Tartu University, now in Canberra, Australia).

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Dr. G. Henningsmoen, Palaeontologisk Museum, Oslo, has on several occasions given highly valuable assistance, and has never hesitated to gratify the author's comprehensive demands as to material or various information.

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GENERAL PART

Terminology

The terminology of the ostracode carapace as adopted in the present paper corresponds essentially to that of Hessland (1949) and Kesling (1951c). In order to achieve sufficient clarity in the taxonomic discussions as well as brevity in the descriptions the creation of some new terms and also the redefinition of some already existing was, however, unavoidable. Some of the new terms have been introduced already in the papers by Martinsson (1955, 1956b) and Jaanusson & Martinsson (1956). Only terms used in the present paper are listed below.

General Terms of the Carapace

The *orientation* adopted in the present paper is that of Bonnema (1909, 1913a, b, 1930, 1932, etc.), Swartz (1936), Triebel (1941), Hessland (1949), Levinson (1950), Kesling (1951c etc.), Henningsmoen (1953a etc.), and others, the adductor muscle scar being situated in front of the transverse line through the middle of the valve. A comprehensive discussion of the characters used for the orientation of the ostracode valve is given, *inter alia*, by Triebel (1941), Hessland (1949, pp. 118–123), and Kesling (1951c).

Longitudinal direction. A direction of the valve or of a part of the valve perpendicular to the direction of the transversal section. In the descriptions the abbreviations (tr.) and (long.) indicate the direction of the length or width of the part of the valve referred to (cf. also Jaanusson & Martinsson 1956).

Domicilium. In ostracodes with adventral or marginal structures or with other ornamental extensions, the carapace exclusive of the ornamental extensions. This term was defined by Kesling (1951c, p. 119) as applying only to ostracodes with "false pouch" (= *dolon*). This restriction seems, however, to

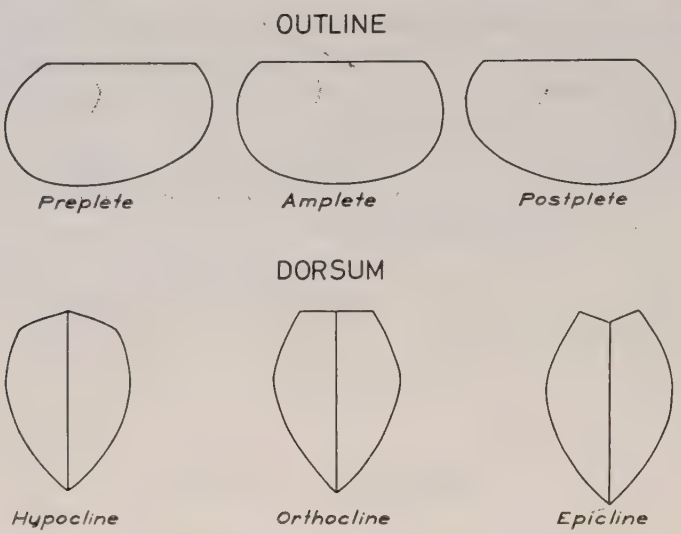

Fig. 1. Illustration of the descriptive terms of the outline and of the dorsum.

be superfluous. The domicilium as defined in the present paper, comprises the parts of the valve which reflect the interior relief of the valve excluding all prominent ornamental extensions (cf. also MARTINSSON 1955, p. 6).

Mid-length and *mid-height*. The transversal and frontal mid-line, respectively, of the valve or of some area of the valve.

Preplete[1] *outline*. Lateral outline of the domicilium in which the greatest height of the domicilium lies in front of the mid-length of the valve (cf. Fig. 1).

Postplete outline. Lateral outline of the domicilium in which the greatest height of the domicilium lies behind the mid-length of the valve. This type of outline has often been called the leperditioid outline.

Amplete outline. Lateral outline of the domicilium in which the heights of the anterior and posterior halves of the domicilium are more or less equal.

Dorsum. A flattened area adjacent to the hinge-line and set off from the lateral surface; in forms with a prominent, ridge-like dorsal plica, the area between the summit of the plica and the hinge-line (cf. Fig. 2). The dorsum may be *epicline*, protruding beyond the hinge-line, *orthocline*, or *hypocline*, not concealing the hinge-line in strictly lateral view (cf. Fig. 1).

Lateral surface of the domicilium. Part of the external surface of the domicilium limited by the lateral margin of the dorsum or, if the dorsum is either poorly defined or absent, by the hinge-line and the histial structure (when

[1] The so-called "plenate terminology" was introduced by SWARTZ (1945, see also SWARTZ & ORIEL 1948). This terminology has been found useful in the above modified form. The ending *-plete* should, however, be substituted for *-plenate*. SWARTZ evidently constructed the element *-plenate* on the basis of a supposed Latin verb *plenare* (= to fill) of which the past participle would be *plenatus* (= *-plenate*). As, however, a root verb (*-*)*plere* already exists, it would be more appropriate to use the participle (*-pletus* = *-plete*) of this verb.

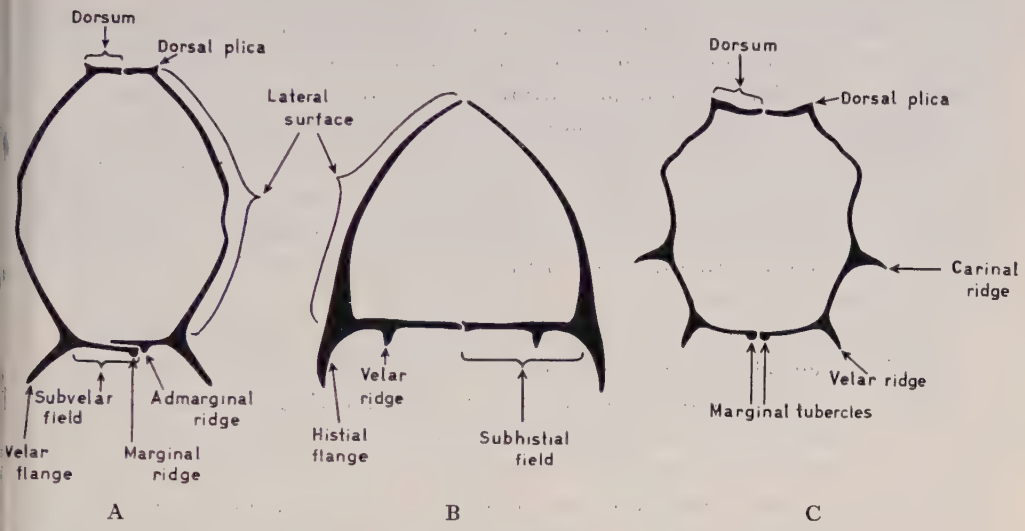

Fig. 2. Diagrammatic transverse sections through ostracode carapaces illustrating some of the terms used in the present paper: A, an eurychilinid carapace; B, a sigmoopsid carapace; C, a bassleratiine carapace, drawn essentially after *Lennukella europaea* (Öpik).

present) or the velar structure (when present, and no histial structure is developed). In forms without any histial or velar structures the lateral surface may be defined by an adventral bend, or the carinal structure, but may also be undefined. Notwithstanding its rather complicated definition the above term has been found very useful in the description of ostracodes, especially of those with a velar or histial structure.

Preadductorial and *postadductorial area.* Part of the lateral surface of the domicilium in non-sulcate valves in front of and behind the transversal line through the adductor muscle scar, respectively; in sulcate or lobate valves in front of and behind S2, respectively (cf. Fig. 3) (cf. also Jaanusson & Martinsson 1956).

Subvelar field. Part of the peripheral surface of the valve limited proximally by the velar structure, and distally by the free edge (cf. Fig. 2). When a histial structure is present the subvelar field forms part of the subhistial field.

Subhistial field. Part of the peripheral surface of the valve limited proximally by the histial structure, and distally by the free edge.

For the other general terms of the carapace not mentioned here, cf. Kesling (1951c).

Terms of the Ornamental Extensions

The terms of certain ornamental structures are further explained in the chapter on the ornamental extensions.

Ornamental structures. Solid extensions of the shell, not leaving any distinct trace internally or upon the internal mould.

Adventral structures. Ridge, flange, or frill-like extensions upon the ventral part of the domicilium situated at some distance from the free edge. The extensions may extend from one cardinal corner to the other, or be confined only to some part of the area along the free edge. From Lat. *ad-*, close to, and *ventral*, referring to the general position of these extensions upon the domicilium. This term is not quite satisfactory, and a more univocal one will probably have to be coined in the future. In the present paper three different types of adventral structures are distinguished, named the velar, the histial, and the carinal structure.

Velar structure. An ornamental ridge, flange, or frill which in quadrilobate valves lies ventral of the connecting lobe, and assumes the corresponding position in non-sulcate or sulcate valves (cf. Figs. 2A–C, 4). Often dimorphic.

Histial structure. An ornamental ridge or flange which in quadrilobate valves forms a direct continuation of the ventral end of the connecting lobe, protrudes in ventral or lateroventral direction, and takes the corresponding position in non-sulcate or sulcate valves (cf. Figs. 2B, 4). Often dimorphic. From Greek ἱστίον, sail.

Carinal structure (in palaeocope ostracodes). Different kinds of non-dimorphic ornamental ridges situated lateroventrally, and often occupying about the same position as the connecting lobe in quadrilobate valves (cf. e.g. Fig. 2C; Kesling & Copeland 1954, Figs. 1E, F).

Dorsal plica. A ridge or crest formed on the boundary between the dorsum and the lateral surface of the domicilium (cf. Fig. 2A, C). It seems advisable in the ostracodes to restrict the term "*plica*" to this structure.

Marginal structures. Ridges, rows of tubercles, or flanges situated on the subvelar field or, in non-velate valves, on the part of the valve roughly corresponding to the subvelar field. If the structure is very close to the free edge it is called *marginal*, if at some distance from it it is called *admarginal* (cf. Fig. 2A, C).

Terms of Lobation and Sulcation

Lobal and sulcal structures. Elevations and depressions of the domicilium which reflect the internal relief of the valve.

Lobes L1, L2, L3, L4 (cf. Fig. 3B). The symbols for the lobes in quadrilobate valves (cf. Hessland 1949, pp. 129–130; Kesling 1951c) and also in valves in which a quadrilobal pattern may be traced. In trilobate valves the lobe behind S2 should not be called L3 as done by Kesling (1951c, p. 117), but might be named L3–4 or Lp (= posterior lobe, cf. Henningsmoen 1954c, Fig. 1, 1955, Fig. 4).

Sulci S1, S2, S3 (cf. Fig. 3B). The symbols for the sulci in quadrilobate valves, and of the homologous sulci in trilobate, bisulcate, or unisulcate valves (cf. Hessland 1949; Kesling 1951c; Henningsmoen 1953a, Fig. 2). S2 bears on a part of the internal side the scar of the adductor muscle.

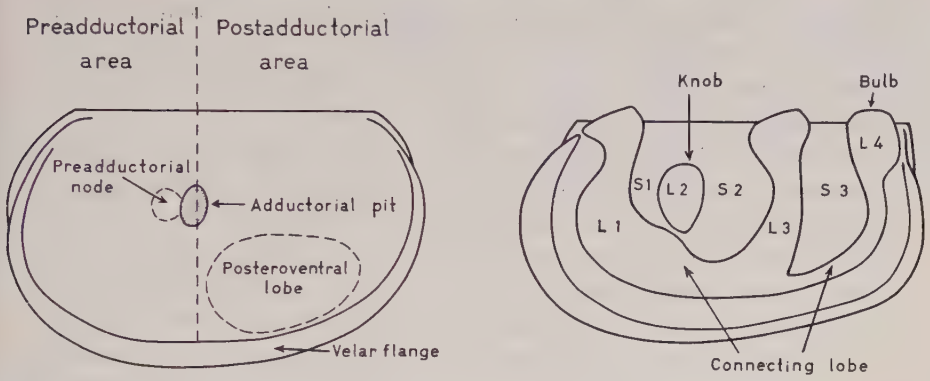

Fig. 3. Illustration of some terms of lobation and sulcation used in the present paper. Further explanation in the text.

Non-sulcate valve. Valve without sulcus or with only a very faint sulcal depression. *Unisulcate valve.* Valve with only one sulcus, a corresponding distinct sulcal depression, or an adductorial pit. In the forms described in the present paper the sulcal structure in unisulcate valves always corresponds to S2. *Bisulcate valve.* Valve in which two sulci are present, or one sulcus and a distinct sulcal depression. The sulci in bisulcate valves referred to in the present paper correspond to S2 and S3. *Trilobate valve.* Valve with 3 lobes or also one in which the trilobation may be clearly traced. *Quadrilobate valve.* Valve with 4 lobes (cf. Fig. 3B) or also one in which the quadrilobation may be clearly traced.

Sulcus. A groove on the external surface of the valve, distinctly expressed as an elevation upon the internal side of the valve. The furrows on the external surface of the valve which do not leave distinct traces in the internal relief of the valve are here usually termed fissures or furrows. Sulcus is also the term for S2 in unisulcate valves.

Sulcal depression. A gentle concavity without distinct borders on the external surface of the valve, being expressed as a faint elevation on the internal side of the valve.

Adductorial pit. A pit in the lateral surface of the valve (cf. Fig. 3A), the corresponding elevation upon the internal side of the valve bearing the scar of the adductor muscle (*Schliessmuskelgrube* Rabien 1954, pp. 38–39; cf. also Martinsson 1955, p. 6).

Lobe. An elongate major protuberance producing a corresponding depression upon the internal side of the valve.

Knob. A rounded, more or less distinctly delimited major protuberance (cf. Fig. 3B). Corresponds to lobe + knob in Kesling (1951c).

Posteroventral lobe. A conspicuous inflation of the ventral part of the post-adductorial area of the domicilium (cf. Fig. 3A) as in *Steusloffia* or *Bolbina.* May correspond to the ventral part of L3. *Anteroventral lobe.* A conspicuous

inflation of the ventral part of the preadductorial area of the domicilium as in some species of *Bolbina*.

Connecting lobe. A lobe connecting the ventral ends of some or of all lobes in quadrilobate valves as in *Tallinnella* (cf. Fig. 3B).

Adventral lobe. A lobe corresponding to L1 + connecting lobe + L4 and not continuous with the ventral ends of L2 and L3. As in *Bollia*.

Preadductorial node. A small node in front of S2 (cf. Fig. 3A) or of the scar of the adductor muscle (presulcate node, HESSLAND 1949, p. 130).

Bend. A rather sharp angulation of the valve, usually producing a corresponding concavity upon the internal side of the valve. If the bend is situated on the boundary between the dorsum and the lateral surface of the valve it is called the *dorsal bend*, if it runs along the free margin, it is termed the *adventral bend*.

Speral process. Hollow extension of the dorsal part of L1, can be shaped as a bulb or a spine. As in *Ceratopsis*, *Sigmoopsis*, and *Glossomorphites*. From Lat. *sperum*, ram.

For the definitions of the terms *sulcation*, *lobation*, *bulb*, *node*, *ventral lobe*, *inflation*, *geniculum*, see KESLING (1951c), and for *semisulcus*, *lobate area*, and *extralobal area*, see HENNINGSMOEN (1953a, pp. 188–190).

Terminology of the Dimorphic Features

This terminology is further explained in the chapter on the dimorphism in the palaeocope ostracodes.

Tecnomorphs. In dimorphic species valves or carapaces of preadult moult stages, and those of the adult stage which are essentially similar to preadult valves. From Greek τέκνον, cub, and μορφή, shape, referring to the similarity between the adult and the preadult valves of this type (see also JAANUSSON & MARTINSSON 1956).

Heteromorphs. Valve or carapace of a supposed female having dimorphic characters not occurring in tecnomorphs.

Kloedenellid dimorphism. Type of dimorphism characterized by an inflation of the posterior part of the female domicilium.

Crumina. A distinct anteroventral or ventral, more or less pouch-like inflation of the domicilium in the female carapace as in beyrichiids (cf. Fig. 4). From Lat. *crumina* = pouch. Previously called "pouch" (cf. KESLING 1951c, p. 119) or also "brood pouch".

Cruminal dimorphism. Type of dimorphism characterized by the development of a crumina in female carapaces as in beyrichiids (cf. Fig. 4).

Dolon. The part of the velar or histial structure which in heteromorphic valves is modified in comparison with that in adult tecnomorphs (cf. also MARTINSSON 1955, p. 6). From Lat. *dolo(n)* = a kind of sail. If formed by a velar structure it is called the *velar dolon*; if by a histial structure, the *histial*

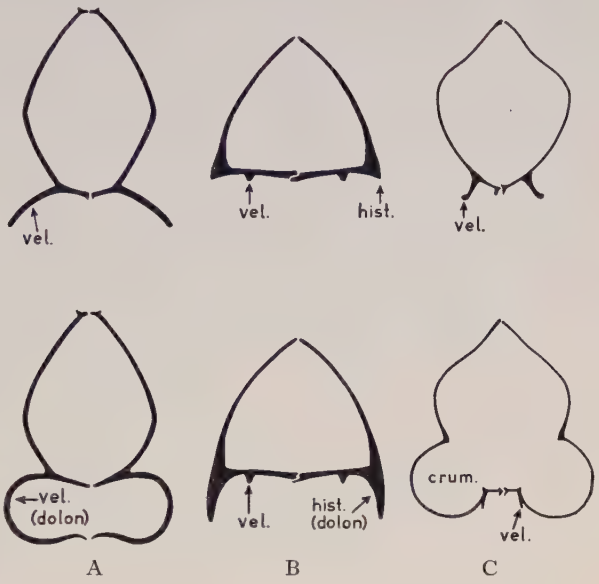

Fig. 4. Diagrammatic transverse sections illustrating the velar (A), histial (B), and cruminal (C) types of dimorphism. *crum.*, crumina; *hist.*, histial structure; *vel.*, velar structure. Tecnomorphs above, heteromorphs below.

dolon. A dolon may be developed as a flange or pouch; in the latter case it has usually been designated by the somewhat contradictory term "false pouch" (cf. e.g. KESLING 1951c, p. 119; for the egg-shaped type he also used the term "pouch", cf. op. cit., Pl. IX, Fig. 7). For the flange-like type of dolon so far no term has existed. There seems to be no need at present to coin special terms for different types of dolon characterized only by shape or extension.

Velar dimorphism. Type of dimorphism in which the velar structure is dimorphic (cf. Fig. 4).

Histial dimorphism. Type of dimorphism in which the histial structure is dimorphic (cf. Fig. 4).

Locular dimorphism. A special type of the histial dimorphism in which the heteromorphs exhibit pit-like depressions (= *loculi*) between the histial flange and the velar structure or, if the velum is missing, between the histial flange and the free edge. As in *Dilobella*, *Tetradella*, *Ctenoloculina*, and related genera. See also pp. 203–204.

The Ornamental Extensions of the Valve

E. A. SCHMIDT (1941) and HESSLAND (1949) suggested that the development of certain ridge- and frill-like extensions of the valve is of greater taxonomic importance than had been assumed previously. The subsequent studies have largely confirmed their suggestions. In order to study the formation of the ornamental extensions of the valve the present writer has examined numerous thin sections, and has tried to follow the ontogenetic development of these

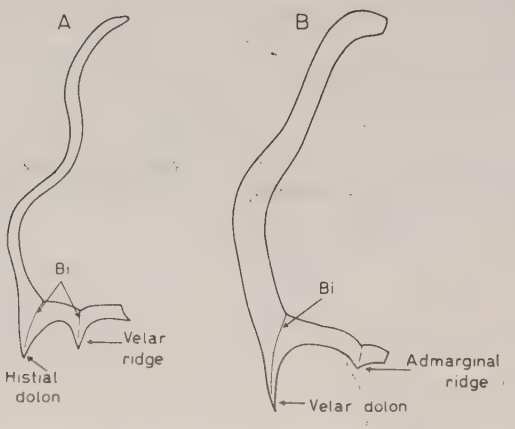

Fig. 5. Diagrammatic drawings after transverse thin sections to illustrate the construction of the adventral structures. × 60. A, *Sigmoopsis platyceras* (Öpik), Estonia, Kukruse, $C_{II}\alpha$; heteromorphic valve. B, *Euprimites effusus* n.sp., Öland, Böda Hamn core, Platyurus limestone, 20.72 m; heteromorphic valve. *Bi*, the line bisecting the adventral extensions. Note the similarity in the position of the velar and histial dolons due to the high placing of the dolonal flange in *Euprimites* in comparison with the tecnomorphic velum in the latter genus and the non-dimorphic velar ridge in *Sigmoopsis*.

extensions in different groups of the *Palaeocopa*. Although this study is still not quite concluded, some of its results are summarized below.

Triebel (1941, pp. 357–358) reported that in thin sections of the "pouch" (= velar dolon) of *Primitiopsis oblonga* (= *Amygdalella subclusa* Martinsson, 1956b) the wall of the "pouch" is seen clearly to be composed of two different layers of the shell. According to him the whole structure corresponds, therefore, to the "zone of concrescence" ("verschmolzene Zone") in podocope ostracodes. A consequence, although not expressed by him, of this statement would be that the subvelar part of the valve in primitiopsids ought to correspond to the duplicature, i.e. that it ought to be formed by the internal layer of epidermis ("inner lamella"). This does not seem to be the case.

Levinson (1951, p. 554) pointed to the common occurrence of a darkened area which bisects the adventral extension of the shell of palaeocope ostracodes studied by him in thin sections. According to the present writer's observations on thin sections all favourably preserved specimens studied exhibit a distinct, often darkened line bisecting the adventral thickening of the shell (cf. Fig. 5, Pl. XIV, Fig. 1). Levinson (op. cit.) concluded that the ornamental extensions were "produced in the living animal by a folding of the mantle-like material with later calcification". According to the present writer's observation on thin sections at least the adventral ornamental extensions of the shell seem in fact to be formed much in the same way as the "zone of concrescence" in *Podocopa*, with the important exception that the fold of the epidermis has evidently been formed by the outer epidermal layer only. The dark line bisecting the extension may in some cases have been formed by the inner chitinous layer of the outer

lamella which has lined the fold internally, and is thus probably, at least in part, analogous to the adhesive strip in the recent ostracodes. Consequently the similarity in the construction of an adventral structure and "the zone of concrescence" seems to result from a similar mode of formation. It ought to be stressed that in the genera in which the bisecting line has been observed no trace of real radial pore canals in the adventral structure occurs although Triebel (1941) supposed to have recognized such canals in *Amygdalella*.

Thus the adventral extensions of the shell are evidently formed by an epidermal fold which by subsequent calcification has produced a solid flange- or frill-like extension. The present writer prefers to make a distinction between the structures which he calls *ornamental*, and which consist of usually solid extensions of the shell, and *lobal and sulcal structures* which reflect the internal relief of the domicilium. The mode of formation of these types of structures is analogous in principle, both being formed by a fold of the epidermis. In the case of lobes the epidermis lines their inner surface, and usually does not cause any secondary thickening of the shell. It is, on the other hand, possible, and in several cases also probable, that coalescence of the epidermis lining both limbs may turn a lobal fold of the epidermis into a solid ornamental extension. In this case the difference between a lobal inflation and an ornamental extension is analogous to that between the monolamellar and the bilamellar types of the marginal area of the ostracodes (cf. Zalányi 1929, Sylvester Bradley 1941) or to that between the regular and isoclinal fold in terms of structural geology. The crests of e.g. *Tallinnellina*, *Rigidella*, and *Steusloffia* have very likely arisen from the regular lobes by constriction and disappearance of the internal lobal cavity as the result of the development of an isoclinal epidermal fold. Other crests, however, e.g. those of *Piretella*, *Rakverella*, and *Hesperidella*, have probably taken their origin from isoclinal epidermal folds without an intervening regular lobe stage. This is made probable by their close connection with the similarly shaped dorsal plica which is often developed as a direct continuation of these crests, and which is never known to be shaped as a lobe. These questions require, however, further study.

The position of the epidermal folds forming lobes, sulci, ridges, crests, and frills upon the valve is in general rather rigidly determined within different groups of palaeocopes and is therefore of great taxonomic importance. The degree of development of these structures may exhibit a rather considerable variation even within one genus, but their location in relation to the general surface of the valve does on the whole not seem to change within a group of related genera.

Special attention has been paid in the course of the present study to the distinction between the different types of ridge- or frill-like extensions near the ventral margin of the valve, designated here with a common term the *adventral structures*. These structures form on the whole a special type of extensions known mainly in the palaeocope ostracodes.

It is quite evident that the ability of forming adventral extensions has been acquired independently in different, remotely related groups of *Palaeocopa*. It is, on the other hand, equally evident that certain of these adventral extensions are homologous in many genera, and that they form, in fact, one of the best criteria for the determination of the relationship within certain palaeocope groups. One of the main problems in the taxonomy of *Palaeocopa* is, therefore, the distinction of homologous from analogous types of adventral structures. This is no easy task as the identical mode of formation tends to produce a very similar external appearance of the different types of adventral extensions, and as, therefore, their real homologies can often be made out by a careful comparative morphological examination of a number of different genera. The greatest taxonomical importance seems to lie in the dimorphic adventral structures.

For the adventral structure, previously named as a rule "frill" or "false border", the term velum was introduced by E. A. SCHMIDT (1941, pp. 13–14). HESSLAND (1949, p. 130) gave a closer definition of this structure, and distinguished another keel-like structure called by him ventral carina. He pointed out that these structures are not homologous, and that they may both be present on the same valve, the velate (= velar[1]) structure occupying a lower, and the ventral carina a higher position in ventral view. Furthermore, according to HESSLAND, the ventral carina corresponds to the ventral "ridge" connecting L1 and L4 of *Tetradella* (= *Tallinnella et al.*) (= connecting lobe in the present paper).

KESLING (1951c, p. 118) distinguishes between the velar structure and the carina, but states that also a velar structure must be present in order to permit a structure to be designated as a carina. A single adventral structure is termed a "velate" structure by him (the same procedure was adopted also by KESLING & HUSSEY 1953, Fig. 1). HENNINGSMOEN (1953a, p. 190) strongly disagrees with KESLING (1951c) as to the definitions of these structures stating that the velar and the carinal structures are not homologous, as pointed out by HESSLAND (1949), and that a carinal structure can be distinguished even when no velar structure is developed. He also agrees with HESSLAND (1949) on the point that L1, L4, and the connecting "ridge" between them may be called a carinal ridge (HENNINGSMOEN 1953a, p. 189, Fig. 2: 2). Of great taxonomic and morphological importance is the statement by HENNINGSMOEN that also the structure termed by him the carinal structure may be dimorphic. This type of dimorphism he calls the carinal dimorphism.

In the present paper three different, obviously non-homologous types of adventral structures are distinguished, which are named the velar, histial, and carinal structures.

Velar structure is used in the same sense as by HESSLAND (1949) and HENNINGSMOEN (1953a). It may be developed as a ridge, flange, or frill, and is

[1] As to the use of velar and velate, see MARTINSSON (1955, p. 6).

frequently dimorphic, being in some of the adult valves broader and more convex than in others, or sometimes pouch-like. In ventral view it occupies a lower position than the other adventral structures as is best seen in forms where the velar structure occurs together with the histial or carinal structure (cf. Figs. 2B, C; 5B) as in *Sigmoopsis*, *Sigmobolbina*, *Carinobolbina*, or *Bassleratia*.

The term ventral carina as defined by Hessland (1949) seems to include several different types of ridge-like structures. All these structures are of the kind termed here the ornamental structures, i.e. thickenings of the shell upon the external surface of the valve. In the opinion of the present writer they cannot be homologized with L1, L4, and connecting lobe, as suggested by Henningsmoen (1953a), the lobes as defined above being inflations of the domicilium.

The ridge-like, often dimorphic, adventral supravelar structure as developed in *Sigmoopsidae* and allied groups is termed here histial structure. In quadrilobate valves the histial structure forms as a rule a direct continuation of the connecting lobe in ventral direction, i.e. the connecting lobe bears on its ventral end the histial structure in form of a ridge-like thickening of the shell. In non-sulcate or unisulcate valves there usually exists a bend on the internal surface of the valve, occupying apparently the same position as the ventral end of the connecting lobe of the quadrilobate valves, and the histial structure is developed as an ornamental thickening of the shell substance projecting ventrally or lateroventrally from the adventral bend (cf. Fig. 2B). In the later forms, however, no bend is developed, and the histial structure may then assume a shape very similar to that of the velar structure from which it, however, differs by its position in relation to the ventral end of the lobes. The histial structure often shows a dimorphism of about the same type as the velar structure, though pouch-like extensions are only seldom formed.

In the present writer's opinion the histial structure is not strictly homologous with similar, but as a rule more dorsally placed, non-dimorphic ridges in *Drepanellinae*, *Bassleratiinae*, or certain *Kirkbyidae* (cf. Kesling & Copeland 1954). The differences in the position between these two kinds of structure can perhaps be illustrated best by stating that the histial structure occupies a position as a ventral ornamental continuation of the connecting lobe, whereas the adventral ridges in *Drepanellinae* and *Bassleratiinae* seem to take the place of the connecting lobe of quadrilobate valves. It seems improbable that the adventral ridge of the drepanellid type should be strictly homologous in the different, only remotely related groups as in *Bassleratiinae*, *Drepanellinae*, or *Kirkbyidae*, and, apart from the shape and, occasionally, also the position, they have certainly nothing in common with similar structures termed *carina* in the *Cytherellidae* or *Cytheridae* (cf. e.g. Bold 1946, p. 11). There seems, on the other hand, to be no need at present to coin special terms for all apparently unrelated types of adventral ridges. The term carina is therefore in the present

paper applied in a wide sense including different kinds of non-dimorphic adventral ridges, not homologous with the velar or histial structures.

It is difficult to give sufficiently concise and exact definitions of the different types of adventral structures since, when only velar, histial, or carinal structures are present, the correct attribution of the structures can evidently be solved only by means of comparative morphological examination. It should be noted especially that in the case of a velar dolon the contact area between the domicilium and the dolon may assume the same position as that between the histial dolon and the domicilium (cf. Fig. 5).

Future studies should be directed especially towards the ontogenetic development of the different adventral structures. Certain observations by the present writer as well as some already published careful studies on the morphology of the moulting stages of the palaeocope ostracodes (Spjeldnæs 1951; Kesling 1952a; Martinsson 1955, 1956b; Adamczak 1956) seem to indicate a possibility of using the differences in the ontogenetic development for a distinction between some adventral structures which are closely similar in the adult stage, but evidently non-homologous.

Most of the adventral extensions are solid thickenings of the shell. In some groups, however, the adventral flange or frill is partitioned internally by radial septa of shell substance into numerous tubules which were obviously hollow during the life of the animal. This type of frill was described by Kesling (1955a) in the hollinacean genus *Oepikium* (cf. also Pl. XIV, Fig. 4). In this genus the junction of the frill with the domicilium does not reveal any perforations leading into the tubules, neither has any peripheral opening been observed. The present studies have shown a similar type of the velar frill to be characteristic for the family *Eurychilinidae* among eurychilinaceans (cf. for a description on p. 230). According to the present state of our knowledge the eurychilinid frill is partitioned internally into a number of narrow radially directed chambers (cf. Pl. XIII, Fig. 5; Pl. XIV, Figs. 6–8), in some genera isolated from the interior of the valve, in others possibly communicating with the latter, but probably always ending blindly at their peripheral end. An identical construction of the velar frill seems to occur also in at least some beyrichiids (e.g. *Beyrichia*, *Apatobolbina*). Moreover, similar but broad internal partitions of the histial flange are described here in the sigmoopsid genus *Oecematobolbina* (cf. Fig. 44).

The above construction of the adventral frill closely resembles that of the recent genera *Puncia* and *Manawa* (cf. Hornibrook 1949). In Hornibrook's description nothing is mentioned about the communication of the chambers of the frill with the interior of the domicilium. According to his figures (Pl. 51, Figs. 1–4) the chambers of the latter genus have no peripheral openings.

The general appearance of the partitions in the eurychilinid frill resembles that of the radial pore canals in certain post-Palaeozoic ostracodes. As, however, the tubules in eurychilinids and in *Oepikium* do not seem to have any external,

and in some cases at least neither internal openings, these tubules can hardly have filled the same function as the radial pore canals. Also their position in relation to the free edge is quite different from that of the radial pore canals which are confined to the duplicature inside the free edge. These types of canals are therefore hardly homologous. The frill of the eurychilinids and of *Oepikium* is usually wide and thin, and the partitions had probably the general function of diminishing the weight of the frill and at the same time of making it stronger mechanically.

Dimorphism in the Palaeocope Ostracodes

The peculiar and rather unique types of dimorphism which have a wide occurrence in the palaeocope ostracodes have been the subjects of much attention and discussion, but only recently the morphology of the different dimorphic characters has begun to be correctly understood. Our knowledge of the dimorphism in these ostracodes is, however, still rather fragmentary, and much careful work remains to be done before the distribution and the significance of the dimorphic characters can be said to be satisfactorily known.

Three major groups of different types of dimorphism can be distinguished in palaeocope ostracodes. The beyrichiid type is characterized by a distinct swelling of the anteroventral or ventral part of the domicilium (= cruminal dimorphism in the present paper) in the adult female valves. This type of dimorphism has been known since R. RICHTER (1869), and has been generally recognized. In kloedenellids and related groups the posterior part of the domicilium is conspicuously inflated in adult female carapaces and thereby they agree with certain recent ostracodes. This type of dimorphism was first described by VEEN (1920) in *Poloniella* (= *Dizygopleura*?) *hieroglyphica* (KRAUSE) and, later, by GEIS (1932, p. 152) in *Glyptopleura parvacostata* GEIS. The careful study by SWARTZ (1933) has shown that the posterior inflation of the adult female carapaces is common, if not universal, in the kloedenellids.

The third major group of dimorphism is characterized by a different development of certain adventral ornamental extensions in a part of adult valves (velar and histial dimorphism in the present paper). The foundation of our knowledge about these types of dimorphism has been laid by BONNEMA (1909) who described and illustrated the dimorphism in a large number of Middle Ordovician species from the Kukruse (="Kuckers") Stage of Estonia, now referred to the genera *Chilobolbina*, *Laccochilina*, *Uhakiella*, *Oepikium*, *Carinobolbina*, and *Sigmobolbina*. He also suggested the probable presence of dimorphism in *Bolbina* (= *Bollia* in BONNEMA 1909). Unfortunately, little attention was paid for a long time to the careful and well-illustrated observations by BONNEMA on the dimorphism of the ornamental extensions, and the different dimorphs, if recognized at all, were still often described as different species.

The posterior velar dimorphism of the primitiopsids was first depicted by Ulrich & Bassler (1923a, Fig. 15: 7–9) in *Primitiopsis planifrons*. Kummerow (1924, pp. 424–425; cf. also Bonnema 1938, pp. 104–105, Figs. 1–19) recorded the presence of a similar dimorphism in *Primitiopsis oblonga* (= *Amygdalella subclusa*, cf. Martinsson 1956b), and Kesling (1951d) in his new genus *Sulcicuneus*. Later the genus *Primitiopsis* was considered as trimorphic by Henningsmoen (1954c, p. 49). Martinsson's (1955, 1956b) subsequent study of the primitiopsids, however, showed *Primitiopsis* as well as his new genera *Clavofabella* and *Leiocyamus* to be clearly dimorphic, the supposed trimorphism being due to the inclusion of certain species of *Clavofabella* in *Primitiopsis planifrons*.

In 1929 Kellett described the supposed trimorphism in several Carboniferous species of *Hollinella* and, later, Swartz (1936, p. 552) suggested *Hollina armata* (Ulrich) and *H. cavimarginata* (Ulrich) to be dimorphs of one species. Warthin (1937, Card 54) suggested the same for *Parabolbina limbata* Swartz and *P. ventrispinosa* Swartz. Kesling & McMillan (1951) defined *Falsipollex* and *Subligaculum* as dimorphic, and Kesling & Tabor (1952) described dimorphism in Devonian species referred by them to *Ctenobolbina* and *Winchellatia* (but probably belonging to new genera).

The peculiar locular dimorphism was recognized first by Warthin (1934) in *Tetradella* (= *Ctenoloculina*) *cicatricosa* Warthin and, later, by Stewart (1936, p. 745) in *Tetrasacculus*. Swartz (1936, pp. 551–552) suggested the occurrence of the same kind of dimorphism in *Dilobella* and *Tetradella*. (This Kay 1940, p. 239, was inclined to regard as isomorphism in *Tetradella*.) Stewart & Hendrix (1945) described *Bisacculus*, Kesling (1952c) *Abditoloculina* (cf. also Kesling 1955 b), Stumbur (1956) *Foramenella*, and Jaanusson & Martinsson (1956) *Triemilomatella* as possessing the same type of dimorphism.

The dimorphism of the ornamental type in Devonian hollinid genera of North America was summarized by Kesling (1952c).

Öpik (1937) described dimorphism in *Piretella*, *Tallinnella dimorpha* Öpik, and *Ceratopsis* (= *Sigmoopsis*), and Thorslund (1940) in *Ctenobolbina* (= *Euprimites*) *suecicus* Thorslund, *Primitia* (= *Levisulculus*) *troedssoni* Thorsl., and *Platychilina* (= *Platybolbina*). Kay (1940) considered the type species of *Eurychilina* to be trimorphic, and described dimorphism in *Euprimitia*, *Winchellatia*, *Bromidella*, *Dicranella*, and in *Conchoprimitia symmetrica* (Ulrich). The last species obviously belongs to a new genus (see also Öpik 1953, p. 33, and Henningsmoen 1953 a, p. 25).

Henningsmoen (1953a) suggested that both species of *Öpikella* (= *Oepikella*) described by Thorslund (1940) are dimorphs of one species, and that certain species of *Glossopsis* (= *Glossomorphites*) described by Hessland (1949) are dimorphs of other species within the same genus (see also Henningsmoen 1954a). According to Henningsmoen (1953a) the different types of valves

distinguished by HESSLAND (1949) within certain species of *Aulacopsis* and *Ctenentoma* (= *Aulacopsis*) *plana* HESSL. are to be considered partly as manifestations of dimorphism. He also stated that according to his observations *Rakverella* obviously possesses a distinct velar dimorphism. Of utmost importance is the recognition, based chiefly on the descriptions of BONNEMA (1909) and ÖPIK (1937), by HENNINGSMOEN of two different types of adventral dimorphism, called by him the velate and the carinal dimorphism (velar and histial dimorphism in the present paper).

Later HENNINGSMOEN (1954a) pointed to the probable existence of dimorphism in *Tallinnella* (= *Protallinnella*) *grewingki* (BOCK) and (1954c) in his new genus *Signetopsis*. MARTINSSON (1956a) figured both dimorphs of *Chilobolbina* (= *Cystomatochilina*) cf. *umbonata* (KRAUSE) (the female type is figured on Pl. II, Fig. 3, not on Pl. II, Fig. 4; cf. MARTINSSON 1956b).

In the present paper dimorphism of the ornamental type is described in some genera in which it was unknown previously (*Hesperidella*, *Polyceratella*), and in the new genera *Piretia*, *Tvaerenella*, *Lomatobolbina*, *Oecematobolbina*, and *Grammolomatella*. The probable presence of a velar dimorphism in *Rigidella* and *Tallinnellina* n.gen. is suggested.

In addition to the above main types of dimorphism also some other dimorphic features have been described. WARTHIN (1937) suggested a certain species of *Bollia* to be a dimorph of another species of this genus. This was, however, doubted by SWARTZ & SWAIN (1941, p. 420). KAY (1940) reported dimorphism in *Opikatia* (= *Oepikatia*) in which in some specimens "there are three swollen nodes along the posterior border of the valve", and in *Bellornatia* which "has similar intramarginal lobes". In *Primitiella* "the anterior (= posterior) half of the female is relatively thickened, rising steeply from the anterior margin". This type of dimorphism resembles that of kloedenellids as pointed also out by KAY (1940, p. 240). HESSLAND (1949) described the probable dimorphism in certain non-velate genera, as in several different species of *Conchoides* (= *Conchoprimitia*) in which the dimorphism is displayed by difference in the width of the posterior part of the carapace and in the ornamentation, and in *Primitiella dibulbosa* where the anterior part of the carapace is higher and broader in one dimorph. LEVINSON (1951) stated some species of *Eridoconcha*, *Cryptophyllus*, and *Milleratia* to be dimorphic, the males according to him being more elongate than the females. All these cases of supposed dimorphism require, however, further confirmation by quantitative investigations.

The intensive study of the palaeocope ostracodes especially in the last years has shown that in several families apparently all genera possess a dimorphism of a certain well-defined type, and that within a genus the dimorphism, if present, occurs invariably in all species. The dimorphic features have, therefore, a great taxonomic importance.

The kloedenellid type of dimorphism is on the whole so similar to that of certain recent ostracodes that there is scarcely any doubt as to which of the

dimorphs is male or female (Veen 1920, Geis 1932, Swartz 1933, and others). As pointed out by Triebel (1941, p. 356) the posterior inflation of the carapace in females is due in recent ostracodes to its function as a breeding room, or, in forms without brood care, to the strong development of the oviduct. In the fossil carapaces it is, according to him, impossible to ascertain which of these factors causes the posterior inflation of the carapace in females.

In order to avoid the use of the term "pouch", often mis-interpreted in the literature on the Palaeozoic ostracodes, the large posteroventral or anteroventral inflation of the domicilium in the beyrichiid ostracodes is in the present paper called a *crumina* (cf. p. 190). The dimorphism of this type is called the *cruminal dimorphism*. The difference between the cruminal dimorphism, in which a part of the domicilium forms a pouch-like structure, and that of the ornamental type, in which a pouch-like structure outside the domicilium is formed by a convex part of the velum or the histium, was known already long ago, but the comparative morphological importance of these differences has not been stressed prior to the papers by Hessland (1949, pp. 123–128) and Henningsmoen (1953a). Hessland (1949, p. 124) and Spjeldnæs (1951, p. 748) succeeded in finding in *Beyrichia* small larval carapaces in the crumina or in its immediate vicinity confirming the assumption that the crumina was used for brood care (cf. also Martinsson 1956b). According to Spjeldnæs (1951) nearly half of the sectioned female specimens of *Beyrichia jonesi* [= *B.* (*Mitrobeyrichia*) *clavata* Kolmodin, cf. Martinsson 1956 b] contained larval valves.

As pointed out by Henningsmoen (1953a) there are two different types of dimorphism in which an adventral ornamental flange is dimorphic: either the velar or the histial structure (= carinal structure *partim* in Henningsmoen, cf. p. 195) can be modified in a part of the adult valves. The corresponding types of dimorphism are termed in the present paper the velar and the histial dimorphism, respectively. The examination of a large material, including both types of dimorphism, has shown the importance of distinguishing between these unrelated, but often rather similar types.

In genera which possess the velar dimorphism, no real histial structure seems ever to be developed. The dimorphism is expressed by a usually broader and more convex velar flange in a part of the adult valves; this modified part of the velar structure is in the present paper called *dolon* (cf. also Martinsson 1955, p. 6). The shape of the dolon varies considerably; it may differ only slightly from the corresponding part of the velar structure in tecnomorphs, or may form a strongly convex flange, the free edges of which may be in contact in closed carapaces. Previously the latter type of the dolon has usually been called "a false pouch". There is, however, a rather gradual morphological series from the dolon developed as a faintly convex flange to that forming a strongly convex "pouch", and there seems at present to be no need of a separate term for the latter type of dolon. In some cases a velar dolon may be developed even if no velar structure is present in the tecnomorphs (as in

Oepikella). The velar dolon may be situated almost anteriorly (as in *Euprimitia*), anteroventrally (as in most genera), ventrally (*Eurychilina*), or posteriorly (*Primitiopsidae*).

The function of the velar dolon and of the velar structure in general has been much discussed. The following interpretations have been suggested: (1) The pouch-like type of dolon serves as a kind of brood pouch (Bonnema 1909, p. 25; Ulrich & Bassler 1923a, p. 278; Öpik 1937; Thorslund 1940; etc.). This idea was strongly criticized by Blake (1930), Triebel (1941, pp. 353–365), and Hessland (1949, pp. 123–128), mainly on account of the external, mostly anteroventral position of these structures which would make difficult the transfer of the eggs into the pouches and prevent the eggs or brood of falling out of them. (2) The frills may have served to protect the appendages when extended from the valves (Blake 1930). This may be true in some cases. If, however, the frill is orientated in almost lateral or ventrolateral direction it is difficult to see the connection between the ventrally and anteroventrally projecting appendages and the frill. (3) They may have served as outriggers in order to prevent the animal from sinking too deep into the soft mud (Blake 1930). In case of broad flanges or frills this function seems very plausible as admitted also by Triebel (1941, p. 361) and Hessland (1949, p. 127). Triebel, however, pointed out that this function can scarcely have been performed by strongly ventromedially curved pouch-like parts of the velum (cf. also Hessland 1949, p. 127). (4) They may have had no function whatsoever (Blake 1930). Some recent species have similar anteriorly situated non-dimorphic flanges as pointed out by Triebel (1941, p. 358, Pl. 13, Fig. 150) which apparently do not have any particular function, except that the free edge is shorter in such a case, and allows a tighter closure. Also in palaeocope ostracodes the non-functional nature of the velar flanges is possible, but not probable. The structure is of common occurrence, and its position upon the valve is so narrowly defined in the *Palaeocopa* that its presence obviously served some purpose. A clear and well-defined sexual dimorphism of the velar structure is, moreover, so wide-spread that it evidently must have fulfilled some function. (5) They may have served for storing the secretion of the marginal glands (Triebel 1941, pp. 361–362). In this case a concentration of the pore canals should be observable in the vicinity of the "pouch" as pointed out by Triebel. Hessland (1949, pp. 127–128) remarked that he saw no trace of such canals and this idea may, therefore, not be tenable. Neither was any such concentration of the pore canals observed by the present writer. (6) The differences in the shape of the velar frill may serve to facilitate copulation (Hessland 1949, p. 127). This may be true, and it appears rather probable for the forms with wide frills, but it is difficult to apply this explanation to species with narrow velar flanges. In forms, where the tecnomorphs have narrow velar ridges, as in *Euprimites*, or no velar structure at all, as in *Oepikella*, the development of a broad dolon in the heteromorphs has in fact the opposite effect.

Summing up, the fact must be stressed that neither the velar structure as such nor the special kind of dimorphism of this structure has any direct counterpart in the recent ostracodes. The only exception seems to be the puzzling family *Punciidae* (Hornibrook 1949) which evidently has a velar frill of the eurychilinid type. Only a few separate valves not showing any dimorphism have as yet been found of this family, but when the animal of this peculiar group will become known, a great many morphological problems of the palaeocope ostracodes will certainly be solved. At present, without any knowledge of the appendages, or other soft parts of the body, all suggestions as to the function of the velar structure and its dimorphism remain highly tentative. The criticism of the "brood pouch" theory by Blake (1930), Triebel (1941), and Hessland (1949) has proved that the velar dolon could not have served as a breeding place. On the other hand, the possibility of its having been used for egg care can, in the present writer's opinion, not be altogether neglected. The appendages in palaeocope ostracodes may have been constructed in the heteromorphs to make possible the transfer of eggs to the shelter of the dolon and their sticking to the wall of the dolon by means of some secretion. The eventuality of the eggs coming into a dangerous proximity to the appendages is probably overrated, since the transversal sections show that the dolon is as a rule placed too high laterally to be reached by the appendages during their normal feeding or locomotory activity. The recent ostracodes usually stick their eggs by means of a viscous secretion to different objects on the bottom of the sea. The velar dimorphism is now known to occur in rather uniform development in a large number of genera, and it is, therefore, probable that it served some essential function, possibly in the reproduction of these forms. The general tendency for the development of the dolon is from a narrow, faintly convex flange to a broad, strongly convex pouch-like structure which certainly offers a better shelter. Usually the contact area between the dolon and the domicilium also moves more in laterodorsal direction, giving the dolon the possibility of attaining greater depth. Also these tendencies speak in favour of the use of the dolon as some kind of shelter.

The histial type of dimorphism is represented either by an expanded histial flange or by the development of a row of large pits ventral to the broadened histial flange (locular type of histial dimorphism). In early forms both histial and velar structures may be developed on the same valve, but as a rule only the histial structure shows the dimorphism. In *Carinobolbina estona* (*Ctenobolbina carinata* in Bonnema 1909), however, neither histial nor velar structure is present in the tecnomorphs (Bonnema 1909, Pl. II, Figs. 15–16), whereas the heteromorphs have a histial as well as a velar ridge. In this case thus both the velar and the histial structures seem to be dimorphic but this cannot be fully ascertained until a closer study of the moult stages has been made. The described tecnomorphs may belong to a preadult moult stage, and the adult

tecnomorphs may possess a velar ridge similar to that in the heteromorphs. A related species, *Carinobolbina? jemtlandica* (THORSLUND), has a well developed velar ridge also in the large tecnomorphs (see THORSLUND 1940, Pl. 4, Fig. 9). In stratigraphically later genera with histial dimorphism frequently no histial structure and also no velar structure at all is present in the tecnomorphs. In these cases it may meet with considerable difficulties to distinguish between the velar and the histial structure, and in some genera it is still unknown whether the flange in the heteromorphs is of histial or velar origin. In all known cases the histial dolon has its strongest development anteroventrally.

When the histial structure is developed as a dimorphic flange the same questions as to its function arise as in the case of the velar structure. Both these structures have, however, evidently the same function, the differences lying merely in their position on the valve. Pouch-like histial dolons are rare, and seem to be known only in *Oepikium* and some Devonian genera.

The peculiar locular type of dimorphism occurring in *Tetradella* or *Ctenoloculina* is believed by the present writer to be a special type of the histial dimorphism. Of both genera mentioned large numbers of specimens have been examined. In *Tetradella* a prominent velar ridge is present. In tecnomorphs (cf. e.g. KESLING & HUSSEY 1953, Pl. II, Figs. 9–10, 15–16, 17–18, 19–20) the velar ridge is normally developed. In heteromorphs the connecting ridge of the crests is expanded in ventral direction, and from these expanded parts thin septa project towards the velar structure, separating a number of large rounded pits between the extension of the connecting crest and the velar structure (cf. e.g. KESLING & HUSSEY 1953, Pl. II, Figs. 11–12, 13–14, 21–22, 23–24). The velar ridge is arched towards the free edge beneath each pit, retaining, however, its tecnomorphic width. The broadened and extended parts of the connecting crest undoubtedly correspond to the histial structure, and *Tetradella* may, therefore, be said to possess a histial dimorphism. As there exists no widening of the velar structure corresponding to that of the dolon of the forms with velar dimorphism, this genus does not seem to possess a velar dimorphism. The downward arching of the velar ridge in the heteromorphs is due probably to the increase in size of the pits in which, we may say, the velar structure has not taken any active part. The above interpretation of the dimorphism in *Tetradella* is further corroborated by the dimorphism in the, in some respects more primitive, but nearly related genus *Dilobella* as illustrated by KAY (1940, Pl. 33). In this genus the velar ridge takes no part in the dimorphism, being developed similarly in both dimorphs. There obviously exists a histial ridge bordering ventrally the lateral surface of the valve (cf. KAY 1940, Pl. 33, Fig. 15) also in the tecnomorphs. In heteromorphs the ridge is anteroventrally expanded, forming a histial flange very similar to that of some sigmoopsids, and anterodorsally septa divide the space between the histial flange and the velar ridge forming some loculi (cf. KAY 1940, Pl. 33, Fig. 11). *Ctenoloculina*

possesses no velar structure, but the formation of the loculi is otherwise similar to that in *Tetradella*. In tecnomorphs flat spurs project ventrally from the anterior three lobes, and the ventral ends of these spurs are obviously to be regarded as histial structures. Heteromorphs possess a broad and thick ornamental flange, connecting the ventral ends of the lobes. This flange resembles the histial dolon in e.g. *Glossomorphites* or *Sigmoopsis* to such an extent as to convince of the fact that it represents a histial structure. Below this histial flange a subdivision by thick septa of the field beneath the protruding histial flange produces a row of loculi (cf. e.g. the illustrations in KESLING 1952a, Pl. I, II, III; 1953a Pl. I and II).

The loculi were interpreted by WARTHIN (1934, p. 209) as "brood pits". TRIEBEL (1941, pp. 358–359) did not believe these pits to have anything to do with reproduction, but suggested no other explanation of their possible function. He also pointed out that the recent *Leptocythere? pavonia* (BRADY) has similar pits which do not serve as "brood chambers". Also KESLING (1952, pp. 265–266) considered it very unlikely that the loculi had been used for brood care. He was led to this opinion by their inadequate size, and by a consideration of the difficulties which an ostracode with appendages like those of living forms would find in transferring eggs forwards from the uterine openings and out of the carapace, and in lodging them firmly in the loculi. According to him the frills of the female of *Ctenoloculina* may have functioned as sled runners with the partitions between the loculi increasing the effective bottom area of the carapace. As the loculi are dimorphic this interpretation would, according to KESLING, involve different biotopes for both dimorphs, the females living benthonic and the males pelagic. The difference of the biotopes for both dimorphs in palaeocope ostracodes had already been suggested by TRIEBEL (1941, p. 362), but was found improbable by HESSLAND (1949, p. 128). In *Ctenoloculina* the present writer believes also the tecnomorphs to be far too thickshelled to make the pelagic mode of living likely.

Examination of a large number of genera with histial dimorphism has shown that the differences between the usual type of histial dimorphism and the locular type are only gradual, the formation of a histial flange in the heteromorphs being common to both types. Both types also show essentially the same kind of dimorphic changes, a part of the adult valves having developed ornamental structures which the other part lacks. For this reason it seems most likely that the function, if any, of both types is on the whole identical. The same suggestion as made and discussed above regarding the velar type of dimorphism may apply thus on the whole also to the particular locular type of the histial dimorphism.

Previously the dimorph with the more complex structure has as a rule been called the female, and the other dimorph with simpler structure the male. HENNINGSMOEN (1953a, pp. 195–196) introduced the terms "female type" and

"male type", "the latter also probably including larval instars and, possibly, unfertilized[1] females".

A fossil population of ostracodes usually consists of a large number of juvenile valves belonging to different moult stages and of a small number of adults of which a part may exhibit the more complex female characters. Without a quantitative study of the moult stages it is often impossible to decide whether a valve without dimorphic characters is an adult male, or a juvenile male or female. During the present investigation it has become apparent that, in order to achieve sufficient clarity, a special term is needed for the valves with the general characters of both the juvenile and the adult male valve. For this purpose the term tecnomorph has been introduced (cf. p. 190) to denote all valves in dimorphic genera which do not show the dimorphic characters of the female type. Valves of the other type can be called adult or mature females, especially in the kloedenellid and cruminal types of dimorphism where their sex can be said to be fairly safely determinable (cf. p. 200). For the velar and histial types of dimorphism, however, the present writer has for the sake of uniformity in descriptions introduced the term *heteromorph* (cf. p. 190) this term denoting specimens with a dimorphic structure not occurring in the tecnomorphs. This term was proposed also on account of the possibility, that the term "adult" or "mature females" may not be correct in all cases as the material studied seems to indicate the presence also of subadult females with female dimorphic characters.

Dimorphism in a species is not safely known until the relation of the supposed heteromorphs to the moult stages of this species has been studied since several cases are known where differences in the development of a structure are due merely to differences between the adult and preadult valves. In *Euprimites suecicus* for instance, the velar ridge of the tecnomorphs seems to be developed mainly in the last moult stage. The supposed trimorphism in the Carboniferous *Hollinella* species described by KELLETT (1929) may also be due to the differences in the development of the adventral structure in older and younger tecnomorphs, KELLETT's non-productive females being adult males. This can, however, not be decided without a quantitative study.

Only a few quantitative investigations on the moult stages of dimorphic palaeocope species have been carried out so far. SPJELDNÆS (1951) described the moult stages in *Beyrichia jonesi* Boll [= *B.* (*Mitrobeyrichia*) *clavata* KOLMODIN, cf. MARTINSSON 1956b]. Cruminate valves of the Mulde population were reported only from the last moult stage (19 adult valves measured), but the

[1] The term "unfertilized" females can often be met with in the literature on the palaeocope ostracodes referring to possible instars of females which had not yet developed the dimorphic characters and which, therefore, cannot be distinguished from the male instars. It is, however, not fertilization itself which produces the dimorphic characters of the valves since these are developed already during the last moulting. This term cannot, therefore, be used in the sense defined above. The correct term would be "juvenile females" or "female instars".

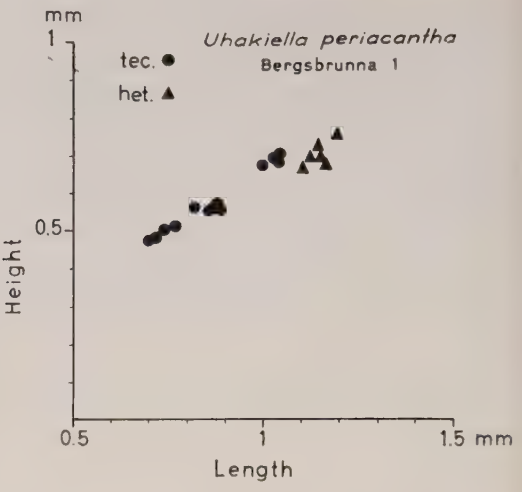

Fig. 6. Size dispersion of the valves of *Uhakiella periacantha* n.sp. from the South Bothnian erratic boulder Bergsbrunna no. 1. Length and height of the domicilium are given. Triangles refer to heteromorphic (*het.*), and dots to tecnomorphic (*tec.*) valves. The valves measured apparently belong to the last three moult stages.

numerical ratio between the adult male and female valves was not given. From another population of the same species he (op. cit., p. 751) recorded the occurrence of some female specimens belonging to the penultimate instar. This appears to be the first reference in literature to a subadult heteromorph of a palaeocope ostracode. SPJELDNÆS suggested that these female specimens "might be interpreted as an early development of sexual dimorphism", but that "it seems more probable that the smaller mature specimens are adults of another population which inhabited a different and perhaps warmer environment".

KESLING (1952a) gave a comprehensive description of the moult stages of *Ctenoloculina cicatricosa* (WARTHIN). Dimorphism was recorded only from the last instar (21 heteromorphs and 6 tecnomorphs measured in this stage). The boundaries between the different moult stages in his material are, however, rather diffuse which points to a rather heterogeneous assemblage. In a later paper (1953b) he described moult stages of the beyrichiid species *Hibbardia lacrimosa* (SWARTZ & ORIEL) in which the dimorphism was also restricted to the last instar (only 2 adult females and 1 adult male were measured).

The most extensive study carried out so far on the moult stages of dimorphic palaeocope species is that by MARTINSSON (1955, 1956b). The ontogeny of three beyrichiid and four primitiopsid species from the Silurian Mulde marl was described in detail. The specimens measured by him were numerous also in the last instar and sex ratios of the dimorphic palaeocopes could be computed in 4 species for the first time. Most of the species studied show the dimorphic characters only in the last instar. In *Clavofabella multidentata* MARTINSSON, however, heteromorphs occur in the two last instars. The last instar of *Clavofabella reticristata* consists of only heteromorphic specimens suggesting that the species was parthenogenetic, and that the dolonate specimens really were females. The populations of one beyrichiid and two primitiopsid species studied

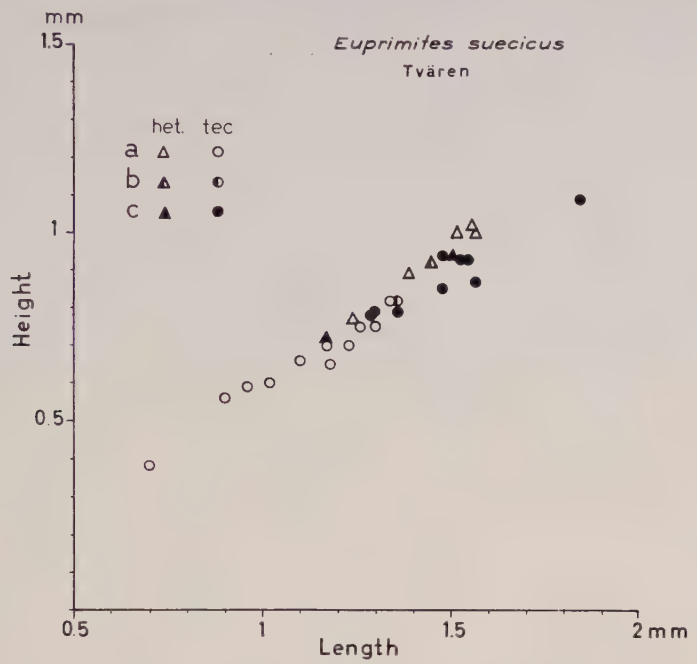

Fig. 7. Size dispersion of the valves of *Euprimites suecicus* (THORSLUND) from the erratic boulders of the Tvären area. Length and height of the valve have been measured in both the tecnomorphs (dots) and heteromorphs (triangles). Legend: Heteromorphs (*het.*): *a*, specimens with comparatively long dolon; *b*, specimens with a dolon of intermediate length; *c*, specimens with comparatively short dolon. Tecnomorphs (*tec.*): *a*, no distinct velar structure present; *b*, velar ridge feebly developed; *c*, a distinct velar ridge present. Note the great variation in size of the heteromorphic valves.

by him have sex ratios in the last instar of about 50: 50 and one primitiopsid species of 30 tecnomorphs to 70 heteromorphs. In the hollinid *Triemilomatella prisca* the sex ratio of about 50: 50 was reported by JAANUSSON & MARTINSSON (1956).

Unfortunately the material described in the present paper was rather unsuitable for studies of the moult stages. Practically all specimens are embedded in the rock, and have to be cleaned with fine needles; during the preparation some damage could seldom be avoided. This applies especially to the very young instars. From some localities, furthermore, the state of preservation of the specimens is not good. Although a rather considerable number of specimens has been examined of several species, the number of valves sufficiently well preserved for measurements can be rather small. Different specimens of a species were usually also derived from different beds, or localities, or areas, and the assemblage measured thus is rather heterogeneous. Only specimens of a species from the same boulder are commonly more homogeneous in this respect, and the different moult stages are then usually rather well distinguished (see e.g. Fig. 6). In other material the different moult stages usually merge more or less continuously into each other (see e.g. Fig. 7).

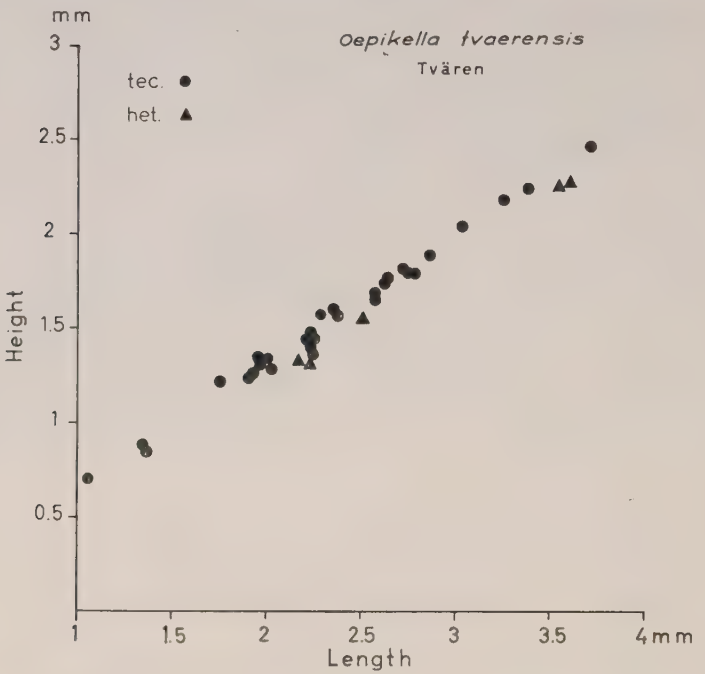

Fig. 8. Size dispersion of the valves of *Oepikella tvaerensis* THORSLUND from the erratic boulders of the Tvären area. Length and height of the domicilium are given. Triangles refer to the heteromorphs (*het.*), and dots to the tecnomorphs (*tec.*). Note the great variation in size of the heteromorphs.

In the recent ostracodes sexual maturity is attained in the last moult stage, and no case is known at present with certainty in which a further moulting takes place after the animal has arrived at sexual maturity (cf. MÜLLER 1926, p. 422; ELOFSON 1941, pp. 398–402). Illustrations of the relation between the female and male valves in the moult stages in some recent species are given by KEY (1954), and its general picture corresponds well to that of *Uhakiella periacantha* n.sp. (cf. Fig. 5). In certain species studied, however, some heteromorphs are smaller than others, and by their size apparently fall within the limits of the last but one moult stage, or into an even earlier moult stage (cf. Figs. 7 and 8). The material studied by the present writer is too heterogeneous to allow of an unambiguous explanation of this phenomenon. The following possibilities must be taken into account: (1) Premature fertility, some animals becoming fertile in an earlier moult stage than usual; (2) further moulting after arriving at sexual maturity, a possibility which, though unconfirmed among the living ostracodes, cannot be entirely excluded; (3) a considerable individual variation between different populations of the species; (4) the material considered here as belonging to one species may in reality belong to several different species which cannot be distinguished through the characters of the valves available to observation. More homogeneous, more numerous, and partly also

better preserved material must be studied in order to reach certainty in this respect.

SUMMARY.—(1) Four different types of dimorphism can be distinguished in the palaeocope ostracodes, called the kloedenellid, cruminal (= beyrichiid), velar, and histial types. The locular type of dimorphism is considered to be a special type of histial dimorphism.

(2) The function of the velar and histial dimorphic flanges is not known at present with certainty. A well-defined, obviously sexual dimorphism of these structures is, however, so wide-spread and uniform that it must evidently have had some purpose to fulfill which in some way or other is connected with reproduction. The possibility that the velar or histial dolon may have been used for egg care cannot, at the present state of our knowledge, be entirely excluded, but these structures had certainly nothing to do with brood care. The possibility that the adult males and females have inhabited different biotopes, and that the dimorphic structure in females may be an adaptation to the different mode of life must also be taken into account although it cannot be proved by the material studied, and is rather unlikely in some cases.

(3) The dimorphic differences in the species hitherto studied in this respect usually occur in the last moult stage. Several cases are, however, known where subadult heteromorphs are found of the size of the penultimate moult stage or even smaller. More material has, however, to be studied, before this phenomenon can be fully understood.

Classification of the Palaeocope Ostracodes

Historical Survey

The first comprehensive account of the classification of the palaeocope ostracodes was given by ULRICH & BASSLER (1923a). Already prior to their paper the following family-group taxa had been erected: *Leperditiidae* JONES, 1856, *Beyrichiinae* MATTHEW, 1886, *Aparchitinae* JONES (in CHAPMAN 1901), *Leperditellidae* and *Kirkbyidae* ULRICH & BASSLER, 1906, *Kloedenellinae* ULRICH & BASSLER, 1907, and *Glyptopleuridae* GIRTY, 1910. ULRICH & BASSLER (1923a) added several families and subfamilies, and presented the following classification:

Family *Leperditiidae* JONES (restricted)
Family *Aparchitidae* new fam.
Superfam. *Beyrichiacea* [new]
Family *Primitiidae* new. fam.
Subfam. *Primitiinae* [new subfam.]
Subfam. *Eurychilininae* new subfam.
Family *Zygobolbidae* new fam.
Subfam. *Zygobolbinae* new subfam.
Subfam. *Kloedeninae* new subfam.
Subfam. *Drepanellinae* new subfam.

Family *Beyrichiidae* Jones (restricted)
Family *Kloedenellidae* new fam.
Family *Kirkbyidae* [Ulrich & Bassler, 1906]

In their classification great taxonomical importance was attached to the characters of sulcation and lobation, and to overlap features. Dimorphic characters were regarded as merely generic, and genera with similar kind of dimorphism were distributed to different families on the basis of their sulcation and lobation. The classification of certain families became, therefore, very schematical, the number of sulci and lobes determining the taxonomical position of the genus as in *Primitiidae* and *Beyrichiidae*. In some other cases, however, natural, well-defined groups were distinguished as in *Kloedenellidae* or *Kloedeninae*.

Swartz (1933, p. 238) pointed out that the differences between the *Kloedenellidae* and the other *Beyrichiacea* seem to be important enough to warrant the removal of this family from the *Beyrichiacea* together with the *Glyptopleuridae*. He also believed that the expansion of the group by further work make it desirable to erect a separate superfamily for the inclusion of these families. He also expressed the opinion (1933, p. 240) that the *Kirkbyidae* ought probably to be removed from the *Beyrichiacea*, but stated that for the time being their classification is uncertain.

Kellett (1933) erected the new family *Youngiellidae*.

The classification given by Bassler & Kellett (1934) corresponds to that of Ulrich & Bassler (1923a) with only minor additions. The subfamily *Glyptopleurinae* Girty, 1910, was added, and for *Leperditiidae* and *Leperditellidae* (including *Aparchites*) the new superfamily *Leperditiacea* was erected.

Bouček 1936 further subdivided the family *Primitiidae* by distinguishing the new subfamilies *Bolliinae* and *Aechmininae*. A new family *Alanellidae* was erected to include a peculiar Lower Silurian genus from Bohemia.

The next comprehensive classification of the palaeocope ostracodes is that of Swartz 1936. According to him the degree of sulcation and lobation is of questionable genetic significance, and has to be used with caution. He also drew attention to the fact that Ulrich & Bassler (1923a) had found it to be relatively unimportant in the *Kloedeninae*, and *Kloedenellinae*. According to his opinion the subventral pouches in certain beyrichiids and eurychilinids represent a more fundamental anatomical structure than the degree of lobation, and one more indicative of genetic relationship. He did not, however, realize that the "pouches" in *Beyrichiidae* and *Eurychilininae* are widely different in construction, and on the basis of the external similarity between these two kinds of "pouches" he transferred the *Eurychilininae* to *Beyrichiidae*. On the other hand, Swartz removed from the *Beyrichiidae* various strongly sulcate genera which lack the pouches and the comparable frills. The family *Primitiidae* was reduced to an assemblage of simply sulcate genera allied to *Primitia mundula* Jones, the type species of *Primitia* as designated by Ulrich & Bassler 1923a, and showing no dimorphism. 4 new families were erected, and the subfamilies *Aechmininae* (the paper of Bouček 1936 being then still unknown to Swartz) and *Drepanellinae* raised to family rank. The families were defined principally on the basis of "supposed relationship inferred from the characters of the ornamentation, including sulci, lobes, frills, and strong persistent spines". The following classification of the genera included by Ulrich & Bassler mainly in the families *Primitiidae* and *Beyrichiidae* was proposed.

Fam. *Beyrichiidae* Ulrich, 1894 (incl. *Eurychilininae*)
Fam. *Primitiidae* Ulrich & Bassler, 1923
Fam. *Hollinidae* Swartz, 1936
Fam. *Tetradellidae* Swartz, 1936

Fam. *Drepanellidae* [Ulrich & Bassler, 1923] Swartz, 1936
Fam. *Aechminidae* [Bouček, 1936] Swartz, 1936
Fam. *Acronotellidae* Swartz, 1936
Fam. *Primitiopsidae* Swartz, 1936

In *Beyrichiacea* Swartz, moreover, distinguished 4 divisions of families as follows:

(1) Division of the family *Primitiidae* including *Primitiidae*, *Hollinidae*, *Tetradellidae*, *Drepanellidae*, *Acronotellidae*, ? *Primitiopsidae*, ? *Aechminidae* (= ? *Leperditacea*). According to him these families lack the subventral dimorphic pouches and the terminal dimorphic swellings; other dimorphic structures are, however, occasionally developed.

(2) Division of the family *Beyrichiidae*, including *Beyrichiidae* (with *Eurychilininae*) and *Zygobolbidae*. Characterized, except in a few primitive genera, by subventral dimorphic pouches.

(3) Division of the family *Kloedenellidae*, including the families *Kloedenellidae* and ? *Glyptopleuridae*. The early genera, at least, develop terminal dimorphic swellings.

(4) Division of the family *Kirkbyidae*, including *Kirkbyidae* and *Youngiellidae*. Characterized by surface sculpture, absence of dimorphic pouches and swellings and, in later genera, by specialized hinge structure.

Swartz concluded that it might prove desirable to regard these divisions as superfamilies, provided that they be supported by further investigations.

On the whole the additions and emendations of the classification of palaeocope ostracodes between Swartz (1936) and Henningsmoen (1953a) can be said to have been less successful, if exception is made for the removal of *Eurychilininae* from *Beyrichiidae*, and the erection and definition of the subfamily *Bassleratiinae* by E. A. Schmidt (1941).

Öpik (1937) erected the new family *Piretellidae* mainly on the basis of the arrangement of ornamental crests.

Kay (1940) gave a new taxonomical arrangement of the *Beyrichiacea* separating the families principally on the basis of the valve lobation. Dimorphism was considered to be of only generic importance. *Eurychilininae* were regarded as a subfamily of *Primitiidae*, and the scope of the subfamily was widened to include all genera with a short sulcus in front of (orientation of Ulrich & Bassler) a rounded node. The new subfamily *Dilobellinae* was erected to include forms with a broad, deep, diagonally extending sulcus.

Swartz & Swain (1941, p. 416) stated that in spite of the fact that a reasonably final classification of Palaeozoic ostracodes is probably still impossible, the return of Kay (1940) to the primary emphasis on the degree or strength of lobation is an undesirable and retrograde step, and leads to unnatural assemblages.

E. A. Schmidt (1941) gave a new comprehensive treatment of the classification of Palaeozoic ostracodes based mainly on studies in literature. The arrangement of Swartz (1936) is on the whole followed, but again more stress is laid on the lobation, the shape of the valve, and also on the development of the velum. Several new subfamilies are erected: *Ctenentominae*, *Ctenonotellinae*, *Bassleratiinae*, and *Ulrichiinae*. In the opinion of Schmidt "stellen *Beyrichiacea* einen mehr oder weniger künstlichen Zusammenfluss von Familien dar, deren Zuordnung in eine der Unterordnungen der rezenten Ostrakoden zur Zeit noch nicht zuverlässig erfolgen kann".

C. I. Cooper (1941) erected the new subfamily *Amphissitinae* within the *Kirkbyidae*.

Triebel (1941, p. 331) pointed out that the impressions of vessels on the inside of the valve in leperditiids undoubtedly represent blood canals, and that leperditiids can therefore be assumed to have had a heart. As among the recent ostracodes this character occurs only in *Myodocopa*, the Palaeozoic forms with blood canals, and consequently

also a heart, may according to him be separated as a special suborder distinguished from the *Myodocopa* by the lack of the rostral incisure.

In an abstract of a still unpublished paper SWARTZ (1945) presented a new classification of the Palaeozoic straight-backed ostracodes. Unfortunately the abstract is in some respects too brief to allow a proper understanding of his ideas. In the classification SWARTZ laid much stress on the type of dimorphism and the lateral outline of the valve. He obviously regarded the location of the "pouch" (crumina) in *Beyrichiidae* as a more important indicator for the orientation than that of the adductor muscle and was, therefore, inclined to consider the cruminate end as the posterior in analogy with the kloedenellids. If according to him "in *Beyrichiidae* the dimorphic pouches are posterior, plenation of the then posterior end indicates morphologic divergence from *Kloedenellidae*, which with their antiplenate pouches are placed in new *Kloedenellacea*". The posterior plenation of *Leperditiidae* suggests morphologic characters reminiscent of *Hymenocaris*; the divergence of the superficially similar *Aparchitidae* is emphasized by the proposed new name *Aparchitacea*.

WARTHIN (1948) drew attention to the fact that the designation of *Beyrichia strangulata* SALTER as the type species of *Primitia* by MILLER (1889, p. 561) antedates all earlier designations known to him of the type species of this genus. Obviously following the suggestion of BASSLER & KELLETT (1934, p. 457) he considered *Beyrichia strangulata* as belonging to *Eurychilina*, and regarded the genus *Primitia* as a senior subjective synonym to it.

SWARTZ (1949) treated the classification of *Leperditiidae* and proposed the new subfamily *Isochilininae*.

HESSLAND (1949) followed on the whole the classification of E. A. SCHMIDT (1941). A new subfamily *Euprimitiinae* was proposed, and included in the family *Hollinidae* as defined by E. A. SCHMIDT in order to restrict *Primitiidae* exclusively to genera without any supermarginal (= adventral) structure.

HORNIBROOK (1949) described two new peculiar genera of recent ostracodes known only from separate valves and astonishingly similar to the Palaeozoic eurychilinids. A new family *Punciidae* was erected for their reception.

SOHN (1950 b) established a new monogeneric family *Miltonellidae*.

A new comprehensive treatment of the classification of the Palaeozoic ostracodes was given by HENNINGSMOEN (1953a). He concluded that the Palaeozoic straight-hinged ostracodes hitherto assigned to the superfamilies *Beyrichiacea* and *Leperditiacea* form a natural group distinct from the recent suborders of ostracodes. For these superfamilies the new suborder *Palaeocopa* was proposed and defined as comprising forms with a usually long and straight hinge-line, no frontal opening, and apparently no calcareous inner lamella. These forms also show a tendency to develop lobes and sulci, and submarginal ridges.

The classification of *Palaeocopa* adopted by HENNINGSMOEN agrees best with that of SWARTZ (1936). The recognition of *Primitia strangulata* (SALTER) as the type species of *Primitia* instead of "*Primitia*" *mundula* (JONES) (WARTHIN 1948) had necessitated corresponding changes of the names of higher taxonomical categories. The type material of *P. strangulata* was subjected to a preliminary examination, and found to be very similar to, if not congeneric with *Uhakiella*. He also pointed out that, as shown already by KUMMEROW (1924, p. 406), the type species of *Ctenentoma* E. A. SCHMIDT, 1941, was erected on an internal mould, possibly of a *Steusloffia* species, and should be regarded as nomen dubium. Thus the subfamily *Ctenentominae* E. A. SCHMIDT, 1941, must also be considered a nomen dubium.

HENNINGSMOEN agrees with SWARTZ (1936) that the degree of sulcation, width and height of lobes and sulci, width of velar structure etc. may vary in closely related forms.

According to him the type of dimorphism, if present, may be of great help in delimiting the suprageneric taxa.

Of great importance was HENNINGSMOEN's recognition of the difference between the velar, and the carinal (= histial) dimorphism. The group of genera with a histial dimorphism or a well-developed histial structure was separated as a special family *Sigmoopsidae*. *Beyrichiidae* were also for the first time clearly defined as consisting of genera with domicilial pouches (= cruminae) in the female type. As to some families or subfamilies distinguished by him too much stress was, however, laid on the supposed relationship inferred from the characters of lobation and sulcation, and the different development of the velum. This is partly due to the then insufficient knowledge of the dimorphism in a great number of genera. The following classification was proposed:

Suborder *Paleocopa* HENNINGSMOEN, 1953
Superfamily *Beyrichiacea* ULRICH & BASSLER, 1923
Fam. *Sigmoopsiidae* HENNINGSMOEN, 1953
Subfam. *Glossopsiinae* HENNINGSMOEN, 1953
Subfam. *Sigmoopsiinae* HENNINGSMOEN, 1953
Fam. *Tetradellidae* SWARTZ, 1936
Subfam. *Tetradellinae* SWARTZ, 1936
? Subfam. *Piretellinae* ÖPIK, 1937
Subfam. *Bassleratiinae* SCHMIDT, 1941
Fam. *Primitiidae* ULRICH & BASSLER, 1923
Fam. *Eurychilinidae* ULRICH & BASSLER, 1923
Subfam. *Eurychilininae* ULRICH & BASSLER, 1923
? Subfam. *Euprimitiinae* HESSLAND, 1949
? Subfam. *Primitiopsiinae* SWARTZ, 1936
Fam. *Aparchitidae* JONES, 1901
Fam. *Drepanellidae* ULRICH & BASSLER, 1923
Subfam. *Drepanellinae* ULRICH & BASSLER, 1923
? Subfam. *Bolliinae* BOUČEK, 1936
? Subfam. *Aechmininae* BOUČEK, 1936
? Fam. *Acronotellidae* SWARTZ, 1936
Fam. *Beyrichiidae* JONES, 1894
Subfam. *Beyrichiinae* JONES, 1894
Subfam. *Zygobolbinae* ULRICH & BASSLER, 1923
Fam. *Hollinidae* SWARTZ, 1936
Fam. *Kloedenellidae* ULRICH & BASSLER, 1908
Subfam. *Kloedenellinae* ULRICH & BASSLER, 1908
Subfam. *Beyrichiopsiinae* HENNINGSMOEN, 1953
Subfam. *Glyptopleurinae* GIRTY, 1910
Fam. *Kirkbyidae* ULRICH & BASSLER, 1923
? Fam. *Youngiellidae* KELLETT, 1933
? Fam. *Miltonellidae* SOHN, 1950
? Fam. *Alanellidae* BOUČEK, 1936
Superfam. *Leperditiacea* BASSLER & KELLETT, 1934
Fam. *Leperditiidae* JONES, 1865
Subfam. *Leperditiinae* JONES, 1865
Subfam. *Isochilininae* SWARTZ, 1949
? Fam. *Leperditellidae* ULRICH & BASSLER, 1906
Subfam. *Leperditellinae* ULRICH & BASSLER, 1906
? Subfam. *Conchoprimitiinae* HENNINGSMOEN, 1953
? Subfam. *Eridoconchinae* HENNINGSMOEN, 1953

As seen from the above list *Conchoprimitia* and allied genera, previously referred to *Beyrichiacea* (Öpik 1937, Hessland 1949), were transferred by Henningsmoen to the *Leperditiacea* chiefly on account of the similarity in the outline and of the absence of a velar structure.

Hessland (1953) substituted the preoccupied generic name *Glossopsis* Hessland, 1949, by the new name *Glossomorphites*. Consequently the name of the subfamily *Glossopsinae* Henningsmoen, 1953, was changed by him into *Glossomorphitinae*.

Kesling & Hussey (1953) erected the new family *Quadrijugatidae* [*recte: Quadrijugatoridae*] to include quadrilobate non-dimorphic forms. As, however, also the genus *Glossopsis* Hessland, 1949 (= *Glossomorphites* Hessland, 1953), type genus of *Glossopsinae* Henningsmoen, 1953[1], was included by them in this family, the family ought to have been called *Glossopsidae* (= *Glossomorphitidae*). They also stressed the great importance of dimorphism as a diagnostic character in certain families of Palaeozoic ostracodes (Kesling & Hussey 1953, p. 80).

Pokorný (1953) regarded *Ostracoda* as a separate class, and subdivided it into four orders: *Beyrichiida*, *Podocopida*, *Myodocopida*, and *Leperditiida*. The order *Leperditiida* was restricted to the family *Leperditiidae* which according to him differs in the presence of a heart and the configuration of the muscle scars considerably from other ostracodes.

Henningsmoen (1954c, p. 52) proposed some alterations in his classification of *Primitiidae* and related groups. *Eurychilininae* and ? *Euprimitiinae* were regarded as subfamilies of *Primitiidae*, and *Piretella* was, as representative of a separate subfamily, transferred into the same family. The remaining *Piretellinae* as delimited by him in 1953a were included into the subfamily *Ctenonotellinae* Schmidt, 1941. *Primitiopsinae* were again considered as a separate family *Primitiopsidae*. *Kloedeninae* Ulrich & Bassler 1923 were anew distinguished as a subfamily within *Beyrichiidae*, and the new subfamily *Treposellinae* added to this family.

Sohn (1954) proposed a new subfamily *Kellettininae* in the family *Kirkbyidae*, and Martinsson (1956b) distinguished the subfamily *Leiocyaminae* within *Primitiopsidae*. Jaanusson & Martinsson (1956) included the hollinids with a locular dimorphism in a separate subfamily *Ctenoloculininae*.

In some papers by Soviet writers several new subfamilies for palaeocope ostracodes have been proposed: *Graviinae* (*Acronotellidae*) by Polenova (1952), *Neodrepanellinae* and *Nodellinae* (both included in *Drepanellidae*) by Zaspelova (1952), and furthermore some new kloedenellid subfamilies by Posner and Egorov, published in papers which have not been available to the present writer.

Classification Proposed in the Present Paper

The classification of fossil ostracodes, in particular of forms which by the morphology of their carapace differ considerably from the recent genera, meets with great difficulties. This is due principally to the fact that only a small portion of the valve around the apodemes of the muscles is in direct contact with the body (cf. Fig. 9; Triebel 1941, Fig. 2), while the remainder of the valve is secreted by the mantle fold which spreads in distal direction from the area of the apodemes. Two different areas can be distinguished in a valve: a central area in contact with the body, and a peripheral area in contact with the

[1] The paper of Henningsmoen 1953a has been published before that of Kesling & Hussey 1953, and the latter had already access to it before their paper was completed.

Fig. 9. Diagrammatic drawing of a female of *Conchoecia magna* (*Halocypridae*) after G. W. Müller 1926, Text-fig. 349. The dotted area of the body is in contact with the valve.

mantle fold. The boundary between these two areas is as a rule rather vaguely indicated upon the valve, and has to be traced with the guidance of the muscle scars. Within the central area are found, in addition to apodemes of different muscles, traces of other organs, particularly the eye, provided this organ was developed, and a part of the impressions of blood vessels within the groups which possess a heart. These questions have been thoroughly and competently discussed by Triebel (1941). The taxonomy of the recent ostracodes is based mainly upon characters of the soft parts of the body. In Cenozoic and Mesozoic ostracodes the pattern of the muscle scars, the features of the duplicature, and those of the hingement have proved of considerable taxonomic significance. In the palaeocopes the duplicature is absent, the hingement is usually simple (cf. Levinson 1950), and the pattern of the individual muscle scars is observable only in exceptional cases. In *Leperditiidae* the latter is usually well preserved, and has also been found to be of considerable taxonomic value (cf. Swartz 1949). In other palaeocopes among the examined material the arrangement of the muscles within the area of the adductor muscle scar cannot be made out, and is, consequently, not available as a systematic character.

The relief and the ornamentation of the valve are preponderantly formed by the mantle fold, and as the latter has obviously the same essential structure in different groups of ostracodes, the possibility of variation of the external characters of the shell is rather limited. Homoeomorphic phenomena are therefore common, externally very similar forms occurring within different taxonomically widely separated groups. For this reason the author fully agrees with the opinion expressed by Swartz (1936) that the degree of sulcation and lobation is of questionable genetic significance, and must be used with caution (cf. also Swartz & Swain 1941, p. 416; Triebel 1941, and Henningsmoen 1953a, pp. 194–195).

In the palaeocope ostracodes, on the other hand, some special characters have a greater taxonomic importance than in the recent suborders. These comprise peculiar types of dimorphism and ornamental extensions which have been

designated by the terms velar and histial structures. Already SWARTZ (1936) had pointed to the obviously great taxonomic value of some of the different types of dimorphism, and these characters have been used with greater consistency by HENNINGSMOEN (1953a) for his taxonomic arrangement of the palaeocope ostracodes.

It can also be pointed out that in several cases the discovery of dimorphism in a genus where it had not been known previously has led to a taxonomic disposition of the genus concerned which differs considerably from that proposed by HENNINGSMOEN (1953a) who had here based his views mainly upon certain characters of lobation. This illustrates still further the uncertainty in the taxonomic arrangement within the palaeocope ostracodes with lobation or ornamentation as a base. The genus *Polyceratella* had been placed by HENNINGSMOEN tentatively among the *Tetradellidae*, whereas the distinct histial dimorphism observed by the present author proves the genus to be a sigmoopsid. *Hesperidella* had been included with the *Bassleratiinae* by HENNINGSMOEN (1953a), but the observed type of dimorphism proved its close connection with *Dicranella* or *Euprimites*. *Bolbina* has been referred by him to *Sigmoopsidae*, but the velar dimorphism and the absence of a histial structure shows its relationship with *Piretella* and allied genera.

In the classification of the palaeocope ostracodes proposed in the present paper the type of dimorphism is regarded as one of the most decisive factors for the disclosure of the relationship between genera. The considerably widened knowledge of the character of dimorphism in many genera for which it was unknown to HENNINGSMOEN (1953a), and a certain re-interpretation of the types of dimorphism in some groups of genera has necessitated several changes in the taxonomic arrangement of the palaeocope ostracodes. The classification of genera in which no dimorphism is developed is much more uncertain and in several cases still open to discussion. In those genera the general presence or absence of a velar structure has been considered to be one of the important taxonomic features.

A major difficulty in the proper classification is the existence of a great number of palaeocope genera which are too incompletely known to allow any closer discussion of their relationship. Special problems arise if such a genus happens to be the type genus for a family-group taxon, as is the case with *Aparchites*, *Acronotella*, and *Ctenonotella*. The writer has found it best at present to regard the family-group taxa of which the type genus is insufficiently known as including only the type genus. When these genera will be more completely known it is possible that the family-group taxa erected on them will prove to be senior synonyms to some of the other taxa considered in the present paper.

Throughout the present paper the decisions on the zoological nomenclature of the XIV International Congress of Zoology, Copenhagen, 1953 (see HEMMING 1953) have been followed. This applies particularly to the family-group

names which are considered to be co-ordinate with one another (HEMMING 1953, p. 33, paragraph 46) including even the superfamily, previously not considered co-ordinate with family or subfamily. Further, the letters with diacritic marks forming an integral part of a specific or generic name has been replaced by a combination of letters representing the diacritic mark in question (HEMMING 1953, p. 79–80, paragraph 155). Thus *Ö* is replaced by *Oe* as in the case of *Oepikella*, *Oepikium*, or *Oepikatia* (named after Prof. A. ÖPIK).

According to information received from Dr. LEVINSON an application will be submitted to the International Commission on Zoological Nomenclature to suppress MILLER's designation of *Beyrichia strangulata* SALTER, 1851, as the type species of *Primitia*, and to preserve the accustomed usage of the genus *Primitia*. As this proposal will hardly be objected to, and as it would be unfortunate if the genus *Primitia* in the sense of HENNINGSMOEN (1953a) would find further spreading in literature, this genus is treated in the present paper in its accustomed usage, i.e. with *Primitia mundula* JONES as the type species. This circumstance has made necessary the re-naming of several family-group taxa distinguished by HENNINGSMOEN (1953a).

In the material examined from the Lower and Middle Ordovician of Baltoscandia three large and apparently natural groups of palaeocope ostracodes can be distinguished: (1) Genera with a histial dimorphism, (2) genera with a velar dimorphism, and related velate forms, and (3) genera without any velar and histial structures. All these three groups appear almost simultaneously in the Arenig, and are distinctly delimited in the Baltoscandian material.

The first of these groups may be provisionally termed the sigmoopsid group. Among Baltoscandian material it corresponds to the family *Sigmoopsidae* of HENNINGSMOEN (1953a) with the exclusion of *Bolbina*, but including *Polyceratella* and *Oepikium*. *Dilobella* and *Tetradella* appear to have a modified type of histial dimorphism as discussed on p. 203. *Dilobella* is also in other respects so similar to certain sigmoopsids that the common features in the dimorphism can hardly be due to convergence. Thus also the family *Tetradellidae* in a restricted sense (including only forms with a locular dimorphism) can be incorporated in this group.

The Devonian genera placed in the family *Hollinidae* by KESLING (1952c) and HENNINGSMOEN (1953a) include those with a locular dimorphism. As stated above (p. 204), according to the present writer's opinion the locular dimorphism should be regarded also in these genera as a special type of histial dimorphism. The loculate hollinid genera have, on the other hand, several characters in common with other hollinid genera which possess only a dimorphic flange. In either case the dorsal part of L3, if developed, is often bulb-like, the adventral structure is as a rule restricted, and there often occurs a spur, mostly isolated in the tecnomorphs, and forming the posterior end of the dolon in the heteromorphs. In the tecnomorphs of *Hollina* the ventral ends of L1 and L3 project in the shape of spurs, and the ventral end of each spur, consisting

of an ornamental thickening of the shell substance, has exactly the same position as that of *Ctenoloculina* and the histial ridge in sigmoopsids. In the heteromorphs the ventral ends of L1 and L3 are united in *Hollina* by an ornamental flange which is rather broad, strongly convex, and pouch-like. As the position of this structure in relation to the lobes is exactly the same as in quadrilobate sigmoopsids and in *Ctenoloculina*, the dimorphic structure in *Hollina* evidently is of histial origin. After having studied a number of specimens of *Falsipollex* and *Hollinella* the writer is convinced that the hollinids display a histial dimorphism, and not the velar dimorphism as thought by HENNINGSMOEN (1953a). At any rate, the dimorphic structure in this family is not of velar origin, and the possibility that it is a third special type of dimorphic adventral structure not strictly homologous with either the velar or the histial structure is rather unlikely at present.

Moreover, some connecting links seem to exist between the mainly Lower and Middle Ordovician sigmoopsids, and the Devonian hollinids. *Tetradellidae* might belong to them, though a direct connection between the members of this family and the Devonian loculate genera cannot be proved at present. From the Upper Ordovician and the Lower Silurian some species have been described which in the present paper are referred to the new hollinid genus *Grammolomatella*. This genus, which undoubtedly possesses a histial dimorphism, also shows a long, sigmoidal sulcus of the general sigmoopsidtype. The Devonian species placed by KESLING & TABOR (1952) and KESLING (1952c) in the genus *Winchellatia*, though in all probability belonging to a new genus, are very similar to certain Middle Ordovician unisulcate sigmoopsids, but evidently represent simple hollinids.

In the present writer's opinion the sigmoopsids, tetradellids, and hollinids are closely related to each other. In addition also *Oepikium* evidently belongs to this main group. With a view to expressing this relationship in the classification, the palaeocopes with a histial dimorphism are regarded as constituting a separate superfamily, called *Hollinacea*. This superfamily includes the families *Sigmoopsidae*, *Tetradellidae*, *Oepikiumidae* nov., and *Hollinidae*. It must, however, be pointed out that this subdivision of the *Hollinacea* into families is at present only tentative, and it is possible that the limits of the families will be changed when more material has been studied.

The type genus of the family *Acronotellidae* is incompletely known at present, but the figures published so far do not seem to exclude the possibility of its belonging to the same superfamily as, and of being closely related to, *Sigmoopsidae*. The lateral view of the type species, *Acronotella shideleri* ULRICH & BASSLER (cf. ULRICH & BASSLER 1923a, Fig. 15: 25; SWARTZ 1936, Pl. 83, Fig. B1a), is very similar to that of some species of *Lomatobolbina* n.gen., and the ventral view (cf. ULRICH & BASSLER 1923a, Fig. 15: 27; erroneously given by SWARTZ 1936, Pl. 83, Fig. B1c as dorsal view) suggests the probable presence of a histial structure. The possibility must even be taken into account

that *Sigmoopsidae* may be a junior synonym to *Acronotellidae*. Yet without an examination of the type species the question about the exact taxonomical position of the genus *Acronotella* cannot be answered at present.

The second main group of related genera among the Baltoscandian material may provisionally be termed the eurychilinid group. In the classification by HENNINGSMOEN (1953a) it corresponds roughly to the following families and subfamilies: *Tetradellidae* (partim), *Piretellinae*, *Bassleratiinae*, *Primitiinae*, *Eurychilininae*, *Euprimitiinae* (partim), and *Primitiopsinae*. Most of the genera included here exhibit a well-developed velar dimorphism, yet the group contains also genera in which no dimorphism has been ascertained, but which all have a distinctly developed velar structure. Certain of these non-dimorphic genera have probably lost the ability of producing dimorphic changes of the velar structure during the evolution (cf. p. 357), and in other cases, as in *Bassleratiinae*, the absence of a velar dimorphism may be a primitive condition.

Within this group five rather distinct subgroups can be distinguished.

(1) The velar structure is a simple, solid, flange- or ridge-like extension which shows a pronounced dimorphism with a well-developed anteroventral or ventral dolon in heteromorphs. This type of velar structure and dimorphism is found in the following subfamilies in the definition of HENNINGSMOEN (1953a): *Primitiinae* (excl. *Chilobolbina*), *Piretellinae* (excl. *Oepikium* which has a histial frill, and *Piretopsis* and *Ctenonotella* which are too poorly known for a settlement of their taxonomic position), furthermore the genera *Euprimitia*, *Euprimites*, *Bolbina*, and *Hesperidella*, placed by HENNINGSMOEN into various other subfamilies. This subgroup is treated in the present paper as a separate family, *Piretellidae*.

(2) The velar structure is partitioned by radial septa into a number of internal, hollow, tube-like chambers. A distinct velar dimorphism with a well-developed dolon is known in all genera. This structure of the velum is characteristic for a group of genera included by HENNINGSMOEN (1953a) in *Eurychilinidae* (incl. *Chilobolbina*).

(3) As in subgroup 1 the velar structure is a simple, solid, flange- or ridge-like extension. Early genera seem to exhibit a simple type of velar dimorphism, the dolon being formed only by a change in the curvature of the velar flange, and by a slight increase in its width. The later genera, in part at least, have probably lost the ability to produce dimorphism in the adult stage. All known genera are quadrilobate or with a clearly traceable quadrilobation. The members of this subgroup were included by HENNINGSMOEN in *Tetradellinae* and *Bassleratiinae*. Here they are united in the subfamily *Quadrijugatorinae*.

(4) The velar structure is non-dimorphic, constructed as in the subgroup 3. In the lobation no quadrilobate pattern can be traced. The exact relationship of this subgroup is at present uncertain, but it may in some way or other be connected with the non-dimorphic genera of the subgroup 3. This subgroup

corresponds to *Bassleratiinae* as defined by E. A. Schmidt (1941) (excluding *Steusloffia*).

(5) Velar structure as in the subgroup 1, but dolon posteriorly situated. This subgroup corresponds to the family *Primitiopsidae* as defined by Swartz (1936), Henningsmoen (1954c), and Martinsson (1955, 1956b).

In addition the genus *Aparchites* may belong to this main group of genera, but the type species of this genus is too poorly known to allow a close comparison with other genera. The possibility that it may possess a velar dimorphism cannot be excluded at the present state of our knowledge, and in this case the family *Aparchitidae* may prove to be a senior synonym to one of the other families with a velar dimorphism.

For this main group the superfamily *Eurychilinacea* has been erected. A reliable subdivision of this superfamily into families is somewhat difficult at present on account of the presence of non-dimorphic genera the exact relationship of which is as yet uncertain. In the present paper the following families are considered to belong to the superfamily *Eurychilinacea: Piretellidae*, *Eurychilinidae*, *Bassleratiidae* (including *Quadrijugatorinae*), and *Primitiopsidae*. *Aparchitidae* are only tentatively referred to this superfamily.

The third major group of genera among the material studied may provisionally be called the leperditellid group. It comprises genera without any velar structure and often with a rather well-defined postplete outline. Dimorphism has been described in several instances, but is of a special type, one dimorph being usually longer and narrower than the other (*Conchoprimitia* in Hessland 1949, *Bollia* in Warthin 1937, *Milleratia*, *Eridoconcha*, *Cryptophyllus* in Levinson 1951). The same phenomenon has been observed also in the material studied by the present writer. Without exact quantitative studies on a representative number of specimens it is, however, difficult to ascertain whether the reported differences are due to dimorphism or merely to individual variation. Similar differences in some species of *Bollia* were regarded by Swartz & Swain (1941, p. 420) as probably due to variation within the species. Unfortunately, no suitable material was available for the study of this question. If, however, the recorded dimorphism exists, this main group would be characterized by its own special type of dimorphism.

Leperditella is apparently closely related to *Conchoprimitia* and the differences are certainly not of subfamiliar value. The material described contains also a rather good morphological series from *Conchoprimitia* and *Primitia* to slightly carinate forms as e.g. *Pyxion* and *Kinnekullea*, and the specimens of *Drepanella*[1] examined clearly show that also this genus belongs to the same

[1] This generic name was consistently spelled "*Depranella*" by Ulrich (1890, pp. 117–121; 1891, pp. 190–191) but later changed into "*Drepanella*" by Ulrich (1897, p. 670) who indicated that the original spelling was due to an error. As pointed out by Ellis & Messina (1952, "*Depranella*", "*Dreṗanella*") and Howe (1955, p. 60) there is no evidence in the original publication that "*Depranella*" represents an error of transcription, a *lapsus calami*, or a typo-

main group, the differences lying mainly in the degree of development of the ornamental characters. The same seems to be the case with *Bollia*. Of *Ulrichia* the present writer has only little first-hand knowledge.

Also *Primitiella* may belong to this main group, but the kloedenellid-like dimorphism described by KAY (1940) has not been observed in the other genera. *Primitiella*-like ostracodes are also among the very first in stratigraphic appearance, and it is well possible that it may be desirable to include them in a group of their own once these forms are better known. In the present paper *Primitiella* is provisionally included in the family *Leperditellidae*.

On the whole the leperditellid group corresponds to the families *Drepanellidae* and *Leperditellidae* in the classification by HENNINGSMOEN (1953a). For this group the superfamily *Leperditellacea* is erected in the present paper.

The present writer cannot join the opinion of several previous authors (BASSLER & KELLETT 1934, HENNINGSMOEN 1953a) that there should exist any closer relationship between the leperditiids and leperditellids. The *Leperditiidae* appear fully differentiated when appearing about simultaneously with the leperditellids, and possess already in the stratigraphically oldest forms the characteristic pattern of muscle insertions (cf. SWARTZ 1949, SCOTT 1951). Furthermore, as pointed out by LEVINSON (1951), the leperditiids have dorsally and ventrally a secondary shell layer, not observed in other palaeocope ostracodes. Also the outline of leperditiids is nearly always considerably more distinctly postplete than that of any leperditellids. The degree of relationship between the *Leperditiidae* and other *Palaeocopa* is in fact as yet little known, and further investigations are needed (cf. also POKORNÝ 1953). In the present paper *Leperditiidae* are considered to belong to a separate superfamily, *Leperditiacea*.

In addition to the superfamilies mentioned, there exist three large Post-Ordovician groups of genera which were already by SWARTZ (1936) suggested as belonging to separate superfamilies. Two of these groups, *Beyrichiidae* and *Kloedenellidae* as defined by HENNINGSMOEN (1953a), possess a distinctive type of dimorphism. The group with cruminal dimorphism is considered in the present paper as the superfamily *Beyrichiacea*, and that with the kloedenellid type of dimorphism as the superfamily *Kloedenellacea*. Of the third group, "the division of the family *Kirkbyidae*" of SWARTZ (1936), the present writer has only a very limited first-hand knowledge. There is no doubt, however, that this group cannot be included in any of the superfamilies mentioned above. It seems best, therefore, to follow the suggestion by SWARTZ (1936), and to regard it as a separate superfamily *Kirkbyacea*.

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graphical error. Although this name has evidently been originally incorrectly transcribed (cf. E. A. SCHMIDT 1941, p. 50) the original spelling cannot be changed without a decision of the International Commission on Zoological Nomenclature. According to the information received from Dr. P. C. SYLVESTER BRADLEY (*in litt.*) an application has been submitted to the ICZN in order to validate the emendation of *Depranella* to *Drepanella*. For this reason the emendated spelling *Drepanella* is used in the present paper.

The classification of the superfamilies *Eurychilinacea*, *Hollinacea*, and *Leperditellacea* will be treated more fully in the chapters of the respective superfamilies.

In the present paper the following classification is proposed (the names within square brackets after the name of the author of the family-group taxon refer to the author of the *nomen translatum*, i.e. to the writer who has changed the concept of the family-group unit in question to a higher family-group category):

Suborder *Palaeocopa* Henningsmoen, 1953
- Superfam. *Eurychilinacea* Ulrich & Bassler, 1923 [nov.]
  - Fam. *Piretellidae* Öpik, 1937
    - Subfam. *Piretellinae* Öpik, 1937
    - Subfam. *Tvaerenellinae* nov.
    - Subfam. *Euprimitiinae* Hessland, 1949
  - Fam. *Eurychilinidae* Ulrich & Bassler, 1923 [Henningsmoen, 1953]
    - Subfam. *Eurychilininae* Ulrich & Bassler, 1923
    - Subfam. *Chilobolbininae* nov.
    - Subfam. *Oepikellinae* nov.
  - Fam. *Bassleratiidae* E. A. Schmidt, 1941 [nov.]
    - Subfam. *Bassleratiinae* E. A. Schmidt, 1941
    - Subfam. *Quadrijugatorinae* Kesling & Hussey, 1953
    - ? Subfam. *Ctenonotellinae* E. A. Schmidt, 1941
  - Fam. *Primitiopsidae* Swartz, 1936
  - ? Fam. *Aparchitidae* Jones, 1901 [Ulrich & Bassler, 1923]
- Superfam. *Hollinacea* Swartz, 1936 [nov.]
  - Fam. *Hollinidae* Swartz, 1936
    - Subfam. *Hollininae* Swartz, 1936
    - Subfam. *Ctenoloculininae* Jaanusson & Martinsson, 1956
    - ? Subfam. *Neodrepanellinae* Zaspelova, 1952
  - Fam. *Oepikiumidae* nov.
  - Fam. *Tetradellidae* Swartz, 1936
  - Fam. *Sigmoopsidae* Henningsmoen, 1953
  - ? Fam. *Acronotellidae* Swartz, 1936
- Superfam. *Beyrichiacea* Matthew, 1886 [Ulrich & Bassler, 1923]
- Superfam. *Kloedenellacea* Ulrich & Bassler, 1908 [Swartz, 1945]
- Superfam. *Kirkbyacea* Ulrich & Bassler, 1906 [nov.]
- Superfam. *Leperditellacea* Ulrich & Bassler, 1906 [nov.]
  - Fam. *Leperditellidae* Ulrich & Bassler, 1906
  - Fam. *Aechminidae* Bouček, 1936 [Swartz, 1936]
  - Fam. *Drepanellidae* Ulrich & Bassler, 1923 [Swartz, 1936]
- Superfam. *Leperditiacea* Jones, 1856 [Bassler & Kellett, 1934]
  - Fam. *Leperditiidae* Jones, 1856
    - Subfam. *Leperditiinae* Jones, 1856
    - Subfam. *Isochilininae* Swartz, 1949
- Inc. superfam.
  - ? Fam. *Punciidae* Hornibrook, 1949

The interrelation of the seven superfamilies of palaeocope ostracodes recognized in this paper is poorly known at present. Four of them, viz. *Leperditiacea*,

Leperditellacea, *Hollinacea*, and *Eurychilinacea*, appear almost simultaneously in the Arenig, and thus their differentiation had evidently taken place already before the appearance of the earliest large ostracode faunas. Also the suborder *Podocopa* makes its appearance at about the same time. Of these four early superfamilies *Eurychilinacea* and *Hollinacea* are certainly more closely related to each other than to the other superfamilies, and have several characters in common, such as the presence of a velar structure, at least in early representatives, and the rather similar pattern of lobation and sulcation. It is, therefore, probable that these groups had a common ancestor. *Leperditellacea* represent the simplest type of the palaeocope ostracodes, and are apparently also the most primitive. It is well possible that the other Ordovician palaeocope superfamilies (*Eurychilinacea* + *Hollinacea* and *Leperditiacea*) have been derived from this group. It ought to be stressed, however, that all these superfamilies are distinctly defined already in the earliest ostracode faunas hitherto described, and that at present no strictly intermediate forms are known. As pointed out above (p. 221) the degree of relationship between *Leperditiacea* and other *Palaeocopa* is uncertain so far, but there exists, on the other hand, no evidence against the possibility of their being derived from leperditellaceans.

Beyrichiacea and *Kloedenellacea* appear first in the Silurian (cf. HENNINGSMOEN 1953a, p. 237; 1954c, p. 36, Fig. 4). According to HENNINGSMOEN (1954c, p. 34–35) the beyrichiids probably developed from the eurychilinids. As the construction of their velar structure seems to be almost identical this assumption appears to be very likely. The velar frill of both eurychilinids and certain beyrichiids is partitioned radially into a number of internal, hollow, tube-like chambers, and this construction of the frill is unknown in other palaeocopes except for *Oepikium* and the puzzling recent family *Punciidae*. The general external appearance of the tecnomorphs of certain non- or unisulcate genera of *Eurychilinidae* and *Beyrichiidae* is remarkably similar (cf. p. 232). The development of the beyrichiids from the eurychilinids involved, however, loss of the external, velar dimorphism and formation of an internal, cruminal dimorphism. Until the course of these important changes is properly understood the exact degree of relationship between these families cannot be said to be known. The origin of the *Kloedenellacea* is much more uncertain. The Ordovician *Primitiella* shows, according to KAY (1940), a similar general type of dimorphism which, if real, may indicate a relationship. In this case, however, the adventral structures in certain kloedenellids may not be homologous with the velar structure in eurychilinaceans, but an independently acquired hacracter, since *Primitiella* and other *Primitiella*-like forms do not possess any trace of such a structure. On the other hand, the type of dimorphism occurring in kloedenellids, and probably also in *Primitiella*, is the simplest and commonest type, wide-spread also in recent suborders, and may have developed quite independently in kloedenellids and *Primitiella*. The relationship of *Kirkbyacea* is uncertain at present, and the Silurian forms of this

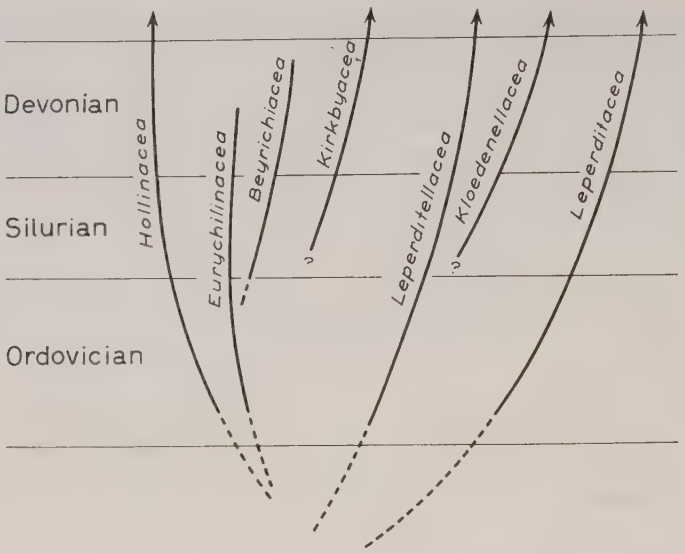


Fig. 10. Diagram illustrating the author's general opinion on the relationship between the different palaeocope superfamilies.

superfamily must be subjected to closer study before this question can be answered.

The author's general opinion about the relationship between the different palaeocope superfamilies is illustrated in Fig. 10.

On the Generic Characters of the Hollinacean and Eurychilinacean Palaeocopes

The concept of genus in the palaeocope ostracodes is still not quite stabilized. This is in part due to the fact that a detailed study of these ostracodes has begun only some decades ago, and that so far only few of the rich and diversified faunas have been described. Almost every new comprehensive treatment of a palaeozoic ostracode fauna results in the discovery of a number of species which cannot be classified with existing generic taxa, and also in a better understanding of the taxonomic importance of different morphological characters which often necessitates splitting or re-grouping of the previously established genera. As far as can be seen this will continue for a long time, and will not end before the main Palaeozoic ostracode faunas are reasonably well known.

In the first comprehensive account on the genera included here in the superfamilies *Hollinacea* and *Eurychilinacea* Ulrich & Bassler (1923a) have attributed great importance to the characters of sulcation and lobation. The shape of S2, for instance, was regarded as generically distinctive, and the forms without a broad frill and with an adductorial pit (like *Laccoprimitia*), with

short sulcus (like *Euprimitia*), or long sulcus (like *Ctenobolbina*) were referred to different genera. The forms with a broad frill (eurychilinids + beyrichiids, *partim*) were classified in a similar way. All distinctly quadrilobate forms without a speral spine or process were included in *Tetradella*, and those with such a process in *Ceratopsis*. Such a rather formal generic classification of a part of the palaeocope ostracodes prevailed for a long time, and is still used to some extent. When, however, other characters, especially the development of the adventral and dimorphic structures had become better known, it also became evident that closely similar to almost identical lobation may have been developed in different, unrelated groups, and that some of the genera in ULRICH & BASSLER's concept in reality represent quite artificial groups. This question is also treated in the chapter on the classification of the *Palaeocopa*.

Nevertheless, distinct differences in the sulcation and lobation are considered of generic importance also at the present state of our knowledge, but first of all the development of the adventral structures must be taken into account before the proper taxonomic position and relationship of a genus can be determined. Moreover, attention ought to be paid to the general trends of variation of the lobal characters. Several instances are known within a closely related group of species where obliteration of certain lobes or sulci produces a continuous change of the lobation or sulcation. Most species of *Ceratopsis*, for instance, are quadrilobate, but in some species the general flattening of the lateral surface of the domicilium results in trilobate to almost unisulcate valves (cf. *Ceratopsis trilobis* KEENAN, 1951, Pl. 79, Fig. 42). Similar variability in respect to the lobation occurs in *Glossomorphites* and *Tallinnella* (cf. p. 341). A number of morphological series illustrating the trend of obliteration of lobes and sulci is described and illustrated by HENNINGSMOEN (1953a, pp. 190–194, Fig. 3). As pointed out by him (op. cit., p. 191), phylogenetic lines from tri- or bisulcate to uni- and non-sulcate forms seem actually to have been established, whereas the opposite is so far not known with certainty.

Apart from the lobation and sulcation also certain ornamental characters, other than adventral, as for instance the arrangement of ridges and crests on the lateral surface of the domicilium, are persistent within a group of related species, and characterize certain genera (cf. *Steusloffia*, *Piretella*, *Hesperidella*).

Experience has shown that in many cases a safe generic reference of a dimorphic species is possible only if both its dimorphs are known. This is due to the fact that several genera are defined by a combination of characters of both dimorphs. Moreover, the best specific characters may be confined to one dimorph, the other dimorph being very similar to, or nearly indistinguishable from other closely related species. This is especially true in respect to material still attached to the rock as it is difficult in such specimens to expose the subvelar or subhistial field, and to reveal the specific characters confined to this field and to the marginal structures. If only tecnomorphs are available it cannot always be ascertained whether they belong to the preadult instars or to

the adult moult stage, and on account of the often rather considerable differences between the adult and preadult instars, especially in the shape of the adventral structure, the species erected on preadult instars are poorly defined or occasionally unrecognizable. On account of the above facts it ought to be avoided as far as possible to erect species of dimorphic genera when one of the dimorphs is unknown. This has been made the rule in the present paper. It should be noted that often a large number of specimens has to be collected before the heteromorphic dimorph will be found, or before the absence of the dimorphism is established, since a fossil population usually consists of a large number of preadult instars and relatively few adult specimens only part of which belong to heteromorphs. For instance only 7 heteromorphs were found among about 60 specimens of *Oepikella tvaerensis*. The composition of several fossil populations of dimorphic palaeocope ostracodes has been discussed and illustrated by SPJELDNÆS (1951), KURTÉN (1953, pp. 48–51), KESLING (1952a), and MARTINSSON (1955, 1956b).

The material studied has shown that distinct differences in the development of the velar and the histial structures usually offer good generic characters. No definite principles for the generic separation can, however, be given. The extension of these structures, in tecnomorphs as well as in heteromorphs, seems nevertheless to be of greater importance than the difference in their relative width. Unfortunately also recent publications on palaeocope ostracodes often give no ventral view of the valve or carapace, and the description of the adventral structures is so cursory that no clear picture of their shape or extension can be obtained. The correct generic reference of species described and illustrated in such a manner is often difficult.

In addition to the sulcal, lobal, ornamental, and dimorphic characters also other features may be of taxonomic importance at the generic level, but they are at present not sufficiently well known in the palaeocopes to be of any practical use. Such characters include hingement and overlap features, marginal structures, and the details of the pattern of the individual muscle apodemes. The great taxonomic importance of these characters is evident from the post-Palaeozoic ostracodes. The hingement features of certain Palaeozoic ostracode genera have been treated by LEVINSON (1951) who also found some of these characters to be of diagnostic value for the delimitation of the genera. On account of its mode of occurrence the material studied unfortunately did not contribute to the knowledge of the hingement of the genera described. In genera with a well-defined adductorial muscle scar (e.g. *Tvaerenella*, *Levisulculus*, *Platybolbina*) the size and location of the latter has proved to be fairly constant within the genus. For this reason in future studies greater attention should be paid to this character in definition of the genera.

DESCRIPTIVE PART

Suborder PALAEOCOPA Henningsmoen, 1953

Syn.: orders *Beyrichiida* + *Leperditiida* Pokorný, 1953.

Diagnosis.—Carapace without either a rostral incisure or siphonal opening. Heart present at least in some groups. Hinge-line straight and usually long. No duplicature known.

Superfamilies.—*Eurychilinacea* Ulrich & Bassler, 1923
Hollinacea Swartz, 1936
Beyrichiacea Matthew, 1886
Kloedenellacea Ulrich & Bassler, 1908
Kirkbyacea Ulrich & Bassler, 1906
Leperditellacea Ulrich & Bassler, 1906
Leperditiacea Jones, 1856.

The recent family *Punciidae* Hornibrook, 1949, exhibits a remarkable similarity to certain palaeocopes, but it is not entirely excluded that this resemblance is due to homoeomorphic development. This possibility is supported by the complete lack of palaeocope-like ostracodes in the Mesozoic and Tertiary strata. In the present paper *Punciidae* are tentatively included in *Palaeocopa* and referred to as *incertae superfamiliae*.

Discussion.—The name of this suborder was given by Henningsmoen (1953a) as *Paleocopa*. As, however, no rules exist concerning the priority of the original spelling of the taxa of the order/class-group category the correct transcription *Palaeocopa* is used thoroughout in the present paper.

Triebel (1941, p. 331) was the first to suggest that at least a part of the groups now included in *Palaeocopa* could be distinguished as a separate suborder of the *Ostracoda*. At the same time E. A. Schmidt (1941) expressed the opinion that *Beyrichiacea* in the sense of Ulrich & Bassler (1923a), i.e. *Palaeocopa* with the exclusion of *Leperditiacea* and *Leperditellacea*, should be regarded as a more or less artificial group of families which on account of the unacquaintance with the morphology of their soft parts cannot be distributed among the recent suborders. The increasing knowledge about the palaeocopes has, however, conclusively shown that some general features of their carapace differ clearly from those of the contemporaneous representatives of *Podocopa*, *Platycopa*, or *Myodocopa*, and characterize a rather well delimited group of its own. The ascertained presence of a heart in some palaeocope families distinguish them also anatomically from *Podocopa*, *Platycopa*, and *Cladocopa*, and the absence of a rostral incisure serves as a distinct difference from *Myodocopa*.

The apparent absence of the duplicature in *Palaeocopa* is at present a character of uncertain value. As far as known the presence of a duplicature has not

been ascertained in any early Palaeozoic *Podocopa* or *Platycopa*, and it is, therefore, possible that the peripheral part of the inner lamella became in these suborders calcified first during a later stage of their evolutionary history. The information about the blood canals and about the probable presence of a heart in the palaeocopes has recently been summarized by HENNINGSMOEN (1954a, pp. 55–57), and will not be repeated here.

The differences between the *Leperditiidae* and the other *Palaeocopa* are probably not so great as suggested by POKORNÝ (1953, 1954, pp. 371–372). The presence of the blood canals is not restricted to the leperditiids only, but has been observed also in *Leperditellacea*, *Beyrichiacea*, and ? *Kloedenellacea* (cf. HENNINGSMOEN 1954a, p. 56). The other distinguishing features mentioned by POKORNÝ have scarcely sufficient importance as to warrant the removal of *Leperditiacea* into a separate suborder (or order).

The classification of *Palaeocopa* has been considered in a special chapter (cf. pp. 214-224).

OCCURRENCE.—Late Tremadocian–Permian (? Recent).

Superfam. EURYCHILINACEA ULRICH & BASSLER, 1923

[*Nom. transl.* JAANUSSON, herein (*ex Eurychilininae* ULRICH & BASSLER, 1923)].

DIAGNOSIS.—Velar structure present, at least in heteromorphs. Most genera exhibit a well defined velar dimorphism. No histial structure.

FAMILIES.—*Eurychilinidae* ULRICH & BASSLER, 1923
Piretellidae ÖPIK, 1937
Bassleratiidae E. A. SCHMIDT, 1941
Primitiopsidae SWARTZ, 1936
? *Aparchitidae* JONES, 1901.

DISCUSSION.—The general classification of *Eurychilinacea* has been considered in the chapter on the classification of the palaeocopes. *Quadrijugatorinae* (*Bassleratiidae*) are the earliest eurychilinaceans known so far and may, as suggested also by HENNINGSMOEN (1953a), be the most primitive group in this superfamily. They possess a simple solid velar frill and obviously also a simple type of velar dimorphism in early genera (cf. p. 357). The later quadrijugatorines are non-dimorphic, but as they have evidently been developed from the probably dimorphic genera the absence of the velar dimorphism may be a secondary condition (cf. p. 357). The earliest *Piretellidae* and *Eurychilinidae* appear only inconsiderably later than the *Quadrijugatorinae*, and the differentiation of these three groups has, therefore, probably taken place already prior to the earliest large ostracode faunas known.

Aparchitidae may represent simple non-dimorphic eurychilinaceans with the velar structure reduced into a ridge, but until a representative number of specimens of the type species of *Aparchites* has been studied the real taxonomic

position of this family remains uncertain. Henningsmoen (1953a, p. 230) suggested that at least some of the forms assigned to *Aparchitidae* developed from *Eurychilinidae* via forms like *Oepikella* by the reduction of the velar structure and the loss of velar dimorphism. However, there is at present no evidence to support this suggestion, and it seems also rather unlikely to the present writer. If *Aparchites*-like forms really are non-dimorphic, and have been developed from dimorphic ancestors it seems more plausible to derive them from *Tvaerenellinae*-like piretellids since the tecnomorphs of some non-sulcate tvaerenellines display a rather close similarity to certain *Aparchites*-like forms. On the other hand, the absence of a velar dimorphism in *Aparchites*, if true, may be a primitive condition, and the family *Aparchitidae* may then constitute the most primitive branch of *Eurychilinacea* or even belong to a superfamily of its own. Further studies are badly needed for answering these questions.

The *Aparchites* problem actualizes an important question in the taxonomy of eurychilinaceans. Theoretically it is namely possible that reduction of the velar structure within some groups of this superfamily has led to non-dimorphic and non-velate forms quite similar in appearance to the leperditellaceans. At present no such forms are known with certainty, but in case they exist it would be difficult to distinguish between these secondarily non-velate descendants of eurychilinaceans and the primarily non-velate and quite unrelated leperditellaceans. The tecnomorphs of *Oepikella*, being non-velate, foreshadow this condition, but have nevertheless a distinct adventral bend by which they can easily be distinguished from the leperditellaceans. Similar forms without an adventral bend would, however, at present be classified with *Leperditellacea*. It is nevertheless probable that future careful studies will reveal new morphological details which will help to define different groups of *Palaeocopa* more closely, and to distinguish between such externally similar, but unrelated forms.

The family *Primitiopsidae* occupies a rather isolated position within *Eurychilinacea*. Other *Eurychilinacea* are mostly or exclusively Ordovician, whereas the primitiopsids are not known at present before the Silurian. The construction of the primitiopsid velar structure and the type of the dolon resemble on the whole those of piretellids, and it seems to be well possible that the primitiopsids have been derived from piretellid-like ancestors.

Occurrence.—The earliest known eurychilinaceans appear in the Arenig and the latest members of this superfamily have been described from Devonian (*Bassleratiinae*, *Primitiopsidae*).

Fam. EURYCHILINIDAE Ulrich & Bassler, 1923

[*Nom. transl.* Henningsmoen, 1953a (*ex Eurychilininae* Ulrich & Bassler 1923)]

Diagnosis.—Non-sulcate to unisulcate. Velar frill partitioned internally by septa of shell substance into numerous, radially arranged tubules which

were apparently originally hollow. Tecnomorphs with either a velar ridge or a frill, or without a velar structure; heteromorphs with a well-developed, more or less convex velar dolon. Tecnomorphic subvelar field low and of a nearly uniform width (tr.) ventrally.

Subfamilies.—*Eurychilininae* Ulrich & Bassler, 1923
Chilobolbininae nov.
Oepikellinae nov.

Construction of the Eurychilinid Frill.—The family *Eurychilinidae* as defined in the present paper differs from other eurychilinaceans mainly by the construction of its velar frill. Immersion of a specimen in some liquid shows clearly that the velum is internally striate (Pl. XIII, Fig. 5; Pl. XIV, Figs. 6–8). A closer examination of this striation shows the frill to be composed of three different elements: (1) an external layer, (2) radial septa, and (3) narrow radial tubules surrounded by these septa and the external layer. A thin layer of shell substance, continuous with the domicilial wall, covers the frill externally as a fold (Fig. 19A). The space between the two limbs of the fold is partitioned by radial septa into numerous narrow tubules which are usually filled with clear calcite. The striation which is visible on immersion of a frill into some liquid is caused by alternating bands of shell substance and clear calcite or some other matter filling the tubules. Originally each tubule was evidently hollow, and the pore space was filled subsequently with mineral substance from solution. In some specimens examined the tubules contained pyrite, and in others hematite.

For the detailed examination of the internal structure of the frill a number of thin sections were prepared through the frill of several eurychilinid species. In general, however, the available material proved so extensively recrystallized as not to reveal details of the internal structure. In some of the thin sections the internal partitions are clearly visible, but it has not been possible to obtain photographs which were sufficiently clear for reproduction.

The above type of velar frill was described previously by Kesling (1955 a) in the hollinacean species *Oepikium tenerum* (Öpik). He stated that in this species the junction of the frill with the rest of the carapace (= domicilium) does not reveal any perforations leading into the tubules. This appears to be true also with regard to the other species of *Oepikium* studied by the present writer. In specimens of *Oepikella tvaerensis* immersed in some liquid, however, narrow tubules give the impression to pierce also the contact area between the domicilium and the velum, and thus to open probably into the interior of the domicilium. In other eurychilinid genera examined the presence of internal openings of the tubules is less certain. A peripheral opening of the tubules has, however, not been observed so far in any specimen. In order to obtain absolute certainty in respect to such minute details of the construction of the frill exceptionally favourably preserved specimens are needed which have not been available.

Thus according to the present state of our knowledge the eurychilinid frill is partitioned internally into a number of narrow, radially directed chambers, in some genera isolated from the interior of the valve, in others possibly communicating with the latter, but probably always ending blindly at their proximal end.

The internal partitions of the frill have been observed in the following genera and subgenera: *Eurychilina*, *Chilobolbina*, *Laccochilina*, *Platybolbina*, *Actinochilina*, *Cystomatochilina*, *Oepikella*, and *Oepikium*. Thus, among the genera placed by HENNINGSMOEN (1953a) in *Eurychilinidae* this structure occurs in all of which specimens have been available, and additionally in *Chilobolbina* and *Oepikium* included by him in other families. As suggested already by ULRICH & BASSLER (1923a) there is, however, no doubt that *Chilobolbina* must be classified with the eurychilinids. The close affinity between *Chilobolbina dentifera* and the species now classified as *Laccochilina* was pointed out also by THORSLUND (1940, p. 166). *Oepikium*, on the other hand, belongs in all probability to the *Hollinacea*. It differs from all eurychilinaceans by the course of the tecnomorphic contact area between the frill and the domicilium, the area ventrally of the frill being very high in both dimorphs (cf. BONNEMA 1909, Pl. V, Figs. 4, 5; ÖPIK 1937, Pl. V, Fig. 4). Moreover, the posterior end of the frill is abrupt, and the sulcus has a shape common in sigmoopsids, but almost never occurring in eurychilinaceans. In these respects *Oepikium* closely resembles the heteromorphs of *Grammolomatella* (cf. p. 406). The high position of the frill of *Oepikium* and other characters make it probable that the frill of this genus is of histial, and not of velar origin. *Oepikium* is, therefore, included in the present paper in *Hollinacea*.

As far as known at present the type of the velar frill described above is restricted within *Eurychilinacea* to the family *Eurychilinidae*. This character provides a more distinct delimination of this family than the characters hitherto used, viz. the degree of sulcation, the relative width of the frill, and, to some extent, the type of dimorphism. Within each genus the coarseness of the partitions of the frill seems to be rather constant. *Laccochilina* (Pl. XIV, Fig. 6), *Platybolbina* (Pl. XIV, Fig. 7), and *Actinochilina* (Pl. XIV, Fig. 8) have rather coarse partitions, in *Chilobolbina* and *Oepikella* (Pl. XIII, Fig. 5) they are comparatively very narrow, and *Cystomatochilina* has partitions of a relative width intermediate between that of *Chilobolbina* and *Laccochilina*.

DISCUSSION.—All eurychilinids hitherto described are non- or unisulcate, and exhibit an advanced velar dimorphism. Certain genera are very similar externally to some piretellids and beyrichiids. The piretellid species *Uhakiella kohtlensis* ÖPIK which has a relatively wide frill closely resembles *Laccochilina* (*Laccochilina*), the main difference between them lying in the construction of the frill. *Piretellidae* and *Eurychilinidae* seem, therefore, to be closely related, Certain species of the eurychilinid genus *Platybolbina* display a close external similarity to tecnomorphs of certain beyrichiid genera, as e.g. *Apatobolbina* and

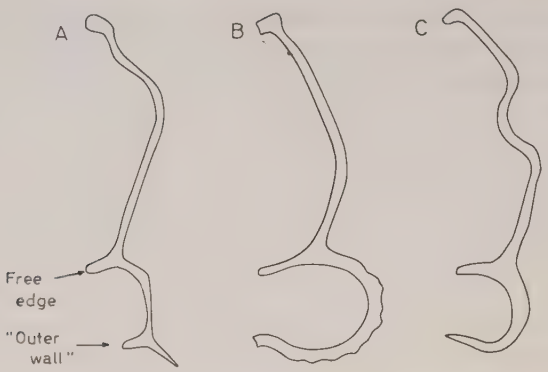


Fig. 11. Transverse sections of heteromorphic valves. A, *Eurychilina subradiata* Ulrich after Ulrich 1897, Pl. XLIV, Fig. 4a; note the prominent "outer wall" of the frill. B, *Chilobolbina sudermannica* n.sp. after the thin section figured by Hessland 1949, Pl. XIV, Fig. 5. C, *Laccochilina* (*Laccochilina*) *paucigranosa* n.sp. after a thin section of a specimen from the South Bothnian erratic boulder Erken no. 10 (cf. Pl. XIV, Fig. 3).

Craspedobolbina. In fact, the main difference between these forms lies in the radically different type of dimorphism, as pointed out by Henningsmoen (1954c, p. 35), and in the cases where the heteromorphic dimorph is unknown at present it is difficult to ascertain whether the species belongs to an eurychilinid or a beyrichiid genus. In early *Beyrichiidae* the details of the construction of the velar frill are still incompletely known, but in some later species of this family at least the frill has evidently the same essential construction as in eurychilinids. However, the Upper Ordovician and Lower Silurian eurychilinids and beyrichiids must be more closely studied before the exact degree of relationship between these families can be said to be known (cf. p. 223).

With respect to the development of the dolon and the velar structure in general three different main groups can be distinguished within *Eurychilinidae*:

(1) The dolon is formed only by the proximal part of the frill, the peripheral part retaining its tecnomorphic shape. On the internal side the dolon is surrounded by a distinct ridge ("outer wall", Ulrich 1897, p. 659) (cf. Fig. 11A). The contact area between the velum and the domicilium occupies in both dimorphs about the same position. Both dimorphs have a velar frill. This type of dolon is known so far only in *Eurychilina*.

(2) The dolon is formed by the entire width (tr.) of the velar frill (cf. Fig. 11B, C); the contact area between the dolon and the domicilium is as a rule situated higher up the side of the valve than that between the frill and the domicilium in tecnomorphs. Both dimorphs have a velar frill. This type of dolon occurs in most eurychilinid genera.

(3) The tecnomorphs have no velar frill at all, whereas the heteromorphs possess a well-developed dolon (cf. Fig. 19). As in *Oepikella*.

The second of the above groups is the earliest to appear and probably also the most primitive. The genera *Eurychilina* and *Oepikella* represent in all

likelihood specialized off-shoots from the second group, derived by the development of an advanced construction of the dolon and by the complete reduction of the tecnomorphic velar structure, respectively. In the present paper the three groups are treated as separate subfamilies.

Occurrence.—The earliest representatives of the family *Eurychilinidae* appear already in the Arenig ($B_{II}\beta$ of Estonia). The members of this family are common in the Ordovician, and some true eurychilinid species have been described also from the Silurian. Frequently Devonian species too have been referred to this family, but in all these cases the family reference is uncertain, and cannot be ascertained without a closer study of the construction of the frill and of the type of dimorphism.

Subfam. CHILOBOLBININAE nov.

Diagnosis.—The dolon is formed by the entire width (tr.) of the velar frill. Both dimorphs possess a velar structure.

Genera.—*Chilobolbina* Ulrich & Bassler, 1923
Coelochilina Ulrich & Bassler, 1923
Apatochilina Ulrich & Bassler, 1923
Laccochilina (*Laccochilina*) Hessland, 1949
Laccochilina (*Prochilina*) n. subgen.
Platybolbina Henningsmoen, 1953
Cystomatochilina n. gen.
Actinochilina n. gen.

Discussion.—Ulrich (1897, p. 659) suggested that the genus *Eurychilina* ought to be restricted to species with "an outer wall" on the marginal area (= velar frill), and was followed in this respect also by Henningsmoen (1953a). The genus *Eurychilina* as represented by the "true species" (Ulrich 1897, p. 659) differs from all genera included here in *Chilobolbininae* by the restriction of its dolon to the proximal part of the velar frill and by the presence of a ridge surrounding the dolon on the internal side of the frill (cf. Fig. 11A). Ulrich (1897, loc. cit.) was inclined to regard the dolonal portion of the velar frill in *Eurychilina* as not homologous with the "false border" (= velum) of other genera, for the reason that he evidently considered the ridge surrounding the dolon to be a domicilial part of the valve. However, the dolon in *Eurychilina* possesses the same internal structure as the other parts of the velum, being partitioned into a number of narrow, radially directed chambers and, therefore, certainly of velar origin. The outer ridge of the dolon seems to be a special velar structure. Restricted as by Ulrich (1897), Henningsmoen (1953a), and the present writer the genus *Eurychilina* has hitherto not been found outside North America. On account of the rather considerable differences between *Eurychilina* and the other *Eurychilinidae* in the construction of the dolon this

genus has been placed by the present writer in a separate subfamily, and the new subfamily *Chilobolbininae* is erected for eurychilinids with a simple dolon and with a distinct velar structure in both dimorphs.

Occurrence.—The occurrence of the subfamily *Chilobolbininae* coincides on the whole with that of the family *Eurychilinidae*.

Gen. *Chilobolbina* Ulrich & Bassler, 1923

Text-fig. 11.

Type Species.—*Primitia dentifera* Bonnema, 1909.

Diagnosis.—Adductorial pit distinct, rounded or ovate, with 8–10 denticles on its inner side. Frill very broad, entire, partitions within the frill comparatively very narrow and numerous. Heteromorphs with a strongly convex, egg-shaped, short dolon.

Species.—*Primitia dentifera* Bonnema, 1909
Chilobolbina sudermannica n.sp.
Chilobolbina lativelata n.sp.

Generic Characters.—Adductorial pit rounded to ovate, well-defined, usually surrounded by a faint rounded ridge. The latter is somewhat elevated in front of the middle of the pit and forms a faint preadductorial node in large specimens. The size of the pit seems to vary even within a species (cf. Pl. I, Figs. 9 and 11). Thorslund (1940, p. 167) found that the pit is distinctly broader in heteromorphs than in tecnomorphs but this is not quite confirmed by the material studied. The pit may be rather small also in heteromorphs (cf. Pl. I, Fig. 11) and large in tecnomorphs (cf. Pl. I, Fig. 8) and it may have the same size in both dimorphs (cf. Pl. I, Figs. 6 and 7). In all species studied the inner margin of the pit is dented by 8–10 triangular denticles.

The surface of the valve is slightly thickened at its dorsal margin forming a low, rounded ridge-like elevation. Cardinal corners flattened, dorsum very low, almost plane, epicline.

The domicilial outline preponderantly somewhat postplete. In the end view the lateral surface of the valve slopes in all species described rather steeply ventrally of the adductorial pit and more gently dorsally of the pit. The change in convexity takes place at about the ventral end of the adductorial pit and is rather pronounced so that the valves of this genus can be easily recognized even when the frill or the pit are not visible. No clear specific differences could be observed as regards outline or convexity.

Velar frill very broad, its height (tr.) about $^{3}/_{8}$ to $^{3}/_{5}$ the height of the lateral surface of the valve, entire, extending from one cardinal corner to the other, broadest ventrally or anteroventrally. It is relatively very thin and easily broken off. The structure of the frill is essentially identical with that of other

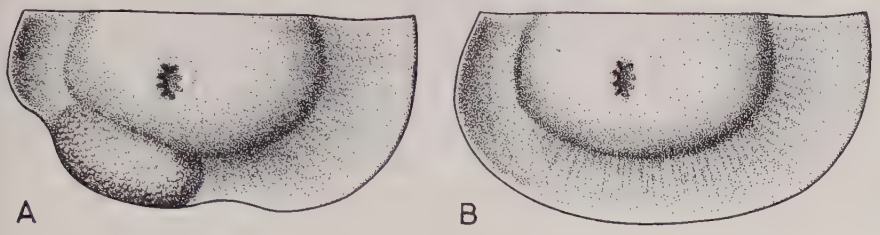


Fig. 12. Reconstruction of a heteromorph (A) and a tecnomorph (B) of *Chilobolbina*. Mainly after *C. sudermannica* n.sp.

eurychilinid genera; the partitions within the frill are, however, considerably narrower and more numerous than in other *Chilobolbininae*. When the frill is broken off a characteristic striated pattern is left on the domicilium along the area of contact between the frill and the domicilial wall (Pl. I, Figs. 4, 5, and Textfig. 13), the ridges corresponding to the laminae of shell substance, and the grooves to the calcite-filled chambers. Striation of this kind has not been observed in any other eurychilinid genus examined.

Fig. 13. Diagrammatic ventral view of a heteromorphic valve of *Chilobolbina sudermannica* n.sp. to show the shape of the contact area between the dolon and the domicilium. After the specimen UM no. T 171 (cf. Pl. I, Fig. 5). × 25.

In tecnomorphs the lateral surface of the frill is concave, except for the foremost part which is faintly convex. The distal part of the frill is almost laterally directed (Pl. I, Fig. 2). Heteromorphs possess a strongly convex, egg-shaped, short dolon. The structure of the dolon of *Chilobolbina* has been discussed by Öpik (1937, Pl. VII, Figs. 2–3), Thorslund (1940, p. 166, Text-fig. 47), and Hessland (1949, Pl. XIV, Fig. 5, Pl. XV, Fig. 21). According to Hessland (1949, p. 126) "the margins of the convex part of the velum seem to lie together when the carapace is closed" (cf. Hessland 1949, Pl. XV, Fig. 21).

In tecnomorphs the contact area between the frill and the domicilium is parallel to the free edge along the entire length of the frill (cf. Pl. I, Fig. 4), whereas in heteromorphs the dolonal part of the contact area forms in lateral view a pronounced curve upwards (cf. Text-fig. 13; Pl. I, Fig. 5). Both valves seem to possess a simple marginal ridge, but the actual closure of the carapace could not be observed as only separate valves were available. The subvelar field is low (tr.) (Pl. I, Fig. 4).

Within the genus *Chilobolbina* the best specific characters seem to lie in the ornamentation of the lateral surface of the domicilium and of the dolon. Also the shape of the frill seems to display specific differences, but these differences cannot at present be clearly defined, the peripheral parts of the frill being usually broken off.

Discussion.—Originally Ulrich & Bassler (1923b, pp. 515–516) included in addition to the type species also *Primitia kuckersiana* Bonn., *Primitia* [= *Platybolbina*] *kapteyni* Bonn., and three Lower Silurian species in their genus *Chilobolbina*. The Lower Silurian species most probably should be classified with beyrichiids as pointed out by Henningsmoen (1953a, p. 227). Öpik (1937, p. 22) restricted the genus to the type species. Thorslund, on the other hand, pointed out that the dolon in *Chilobolbina* has on principle the same construction as in *Primitia* [= *Laccochilina* (*Prochilina*)] *decumana* Bonn. and *P. kuckersiana* Bonn., the differences lying merely in the degree of the convexity and of the extension of the dolon. As he did not consider the latter characters to be of generic value, he included the above-mentioned species in *Chilobolbina*.

In the present paper Öpik's delimination of this genus is adopted. Apart from the egg-shaped dolon there are also several other characters, as for instance the very broad frill and the persistent presence of the denticles in the adductorial pit, which unite a well-defined, natural group of species.

Occurrence.—The genus *Chilobolbina* has been found in the Lower Ordovician *Platyurus* limestone and in the Middle Ordovician *Schroeteri*, *Crassicauda*, and *Ludibundus* limestones of Sweden, and in the Kukruse Stage of Estonia. Outside of Sweden and Estonia this genus has been recorded so far only from the North German erratic boulders.

Chilobolbina dentifera (Bonnema, 1909)

Pl. I, Figs. 6–7.

1909 *Primitia dentifera* n.sp.—Bonnema, pp. 25–26, Pl. II, Figs. 1–5.
1923a *Chilobolbina dentifera* (Bonnema)—Ulrich & Bassler, p. 303, Fig. 16 (1–2) (reconstruction after Bonnema 1909, Pl. II, Figs. 1–4).
1933 *Chilobolbina dentifera* (Bonnema)—Bonnema, p. 36, Figs. 34, 35 (copied from Ulrich & Bassler 1923a, p. 303, Fig. 16: 1–2).
1934 *Chilobolbina dentifera* (Bonnema)—Bassler & Kellett, p. 244, p. 21, Fig. 7 (1–2) (copied from Ulrich & Bassler 1923a, Fig. 16: 1–2).
1937 *Chilobolbina dentifera* (Bonnema)—Öpik, p. 22, Pl. VII, Figs. 1–3.
1951c *Chilobolbina dentifera* (Bonnema)—Kesling, Pl. IX, Figs. 7–8 (after Ulrich & Bassler 1923a).
1954 *Chilobolbina dentifera* (Bonnema)—Pokorný, p. 386, Fig. 500 (after Bassler & Kellett, p. 21, Fig. 16: 1–2).
1955 *Chilobolbina dentifera* (Bonnema)—Sarv, p. 13.
1956a *Chilobolbina dentifera* (Bonnema)—Sarv, p. 47.
? non *1924* *Chilobolbina dentifera* (Bonn.) sp.—Kummerow, p. 441 [– ? *Chilobolbina lativelata* n.sp.]
non 1940 *Chilobolbina dentifera* (Bonnema)—Thorslund, p. 167, Fig. 57: 3–4, Pl. 1, Figs. 1, 2 [= *Chilobolbina sudermannica* n.sp.].
non 1949 *Chilobolbina dentifera* (Bonnema)—Hessland, p. 126, Pl. XIV, Fig. 5, Pl. XV, Fig. 21 [= *Chilobolbina sudermannica* n.sp.].
aff. *1953* *Chilobolbina dentifera* (Bonn.)—Jaanusson, p. 417.

LECTOTYPE (here chosen).—Right heteromorphic valve, TM no. Os-2302, figured by BONNEMA 1909, Pl. II, Fig. 3.

TYPE LOCALITY.—Kukruse ("Kuckers"), Estonia.

TYPE STRATUM.—Middle Ordovician, Kukruse Stage (C_{II}), probably its lower zone ($C_{II}\alpha$).

MATERIAL.—4 tecnomorphic valves, 1 heteromorphic valve.

DIAGNOSIS.—Length of the lateral surface of heteromorphs 1.5–1.6 mm. Ornamentation consisting of a faint, fine-meshed reticulation in front of and behind the adductorial pit; no evident reticulation on the ventral part of the lateral surface. Dolon with moderately large, closely set tubercles except for a narrow, radially striated part adjacent to the domicilium.

SPECIFIC CHARACTERS.—Outline of the lateral surface almost amplete; highest convexity of the valve somewhat behind the adductorial pit.

The figures of this species published by BONNEMA (1909) and ÖPIK (1937) do not show the details of the ornamentation. Neither did they describe the ornamentation in the text. The specimens from the type locality and other neighbouring localities studied by the present writer possess a characteristic ornamentation. The inner part of the lateral surface of the domicilium in front of and behind the adductorial pit is faintly and finely reticulated (cf. Pl. I, Figs. 6, 7). Ventrally, and occasionally also dorsally, of the pit no reticulation is visible, and the ornamentation there consists, on some specimens at least, only of a few scattered tubercles which form an irregular row close to the dorsal margin of the valve.

According to the measurements given by BONNEMA (1909, p. 25) the height (tr.) of the frill along the mid-length of the valve is about $^3/_8$ of the height of the lateral surface of the domicilium. The dorsal ends of the frill do not seem to protrude beyond the dorsal margin of the valve (cf. BONNEMA 1909, Pl. II, Fig. 2). In this respect *C. dentifera* is similar to *C. sudermannica* n.sp. The frill of the former species seems, however, to be more fragile and thinner than in the latter. The proximal narrow part of the dolon adjacent to the domicilium is radially striated (cf. Pl. I, Fig. 6; ÖPIK 1937, Pl. VII, Fig. 1). The other parts of the dolon are covered with moderately large, closely spaced tubercles which are much smaller and more numerous than in *C. sudermannica*.

DISCUSSION.—As pointed out by THORSLUND (1940, p. 167) the previously published reconstructions of this species (ULRICH & BASSLER 1923a, p. 303, Fig. 16: 1–2, copied by BONNEMA 1933 and BASSLER & KELLETT 1934; redrawn by KESLING 1951c and POKORNÝ 1954) are not quite satisfactory. A new reconstruction of *Chilobolbina* (mainly after *C. sudermannica* n.sp.) is given in Text-fig. 12.

In the *Crassicauda* limestone of Sweden a species of *Chilobolbina* very similar to *C. dentifera* has been found in several districts. The frill of these specimens is thin and fragile, and resembles in this respect that of *C. dentifera*, the surface of the domicilium is, however, apparently smooth without any

trace of reticulation. The ornamentation seems to consist only of a few small scattered tubercles. Unfortunately only tecnomorphs and one fragmentary heteromorph have been found so far, and the shape and ornamentation of the dolon are unknown. Until more complete heteromorphs have been encountered this smooth *Chilobolbina* species from the *Crassicauda* limestone will be referred to as *C.* aff. *dentifera*.

Occurrence.—*Chilobolbina dentifera* has up to now been found with certainty only in the Kukruse Stage (C_{II}) of Estonia. The species has been reported from Kukruse ("Kuckers") and Kohtla-Järve.

C. aff. *dentifera* occurs in the *Crassicauda* limestone: *South Bothnian district*. —Erratic boulders Erken no. 10 (5 tecnom.) and Bergsbrunna no. 1 (5 tecnom.). *Öland*.—Böda Hamn bore (1 tecnom.). *Östergötland*.—Motala bore (1 tecnom.); Smedsby Gård bore (1 heterom.).

Chilobolbina sudermannica n. sp.

Pl. I, Figs. 1–5; Text-figs. 11B, 13.

1940 *Chilobolbina dentifera* (Bonnema)—Thorslund, p. 167, Fig. 57: 3–4, Pl. 1, Figs. 1, 2.

1949 *Chilobolbina dentifera* (Bonnema)—Hessland, p. 126, Pl. XIV, Fig. 5, Pl. XV, Fig. 21.

Holotype.—Left heteromorphic valve, UM no. T 141, figured on Pl. I, Fig. 3.

Type Area.—Tvären area, Ringsö, erratic boulders.

Type Stratum.—Lowermost part of the *Ludibundus* limestone.

Derivation of the Name.—After Södermanland, the province in which the type area of the species is situated.

Diagnosis.—Length of the lateral surface of the domicilium in the heteromorphs 1.7–1.8 mm. The whole lateral surface ornamented with a distinct, rather coarse reticulation. Dolon with large, somewhat irregular tubercles except for a narrow, smooth or very faintly radially striate part adjacent to the domicilium.

Material.—7 heteromorphic and 16 tecnomorphic valves.

Specific Characters.—Outline and convexity as in *C. dentifera*. On all specimens examined the ornamentation of the lateral surface of the domicilium consists of a distinct, rather coarse reticulation covering the whole lateral surface with the exception of a very narrow area adjacent to the dorsal margin and of the ridge-like elevation around the adductorial pit. Apart from the reticulation the ornamentation includes a small number of widely scattered tubercles which are more closely spaced near the dorsal margin, forming there an irregular row.

Table 1.

No.	UM Mus. cat. no.	L. domic.	H. domic.	H-L	Valve	Remarks
1	T 169	1.78	0.96	~1.48	h—r	
2	T 141	~1.74	~1.00	—	h—r	Holotype. Pl. I, Fig. 3.
3	T 172	1.74	1.00	1.55	h—l	
4	T 171	1.68	0.94	—	h—l	Figured on Pl. I, Fig. 5.
5	T 170	1.78	0.89	—	t—l	
6	T 166	1.56	0.86	—	t—l	
7	T 173	1.51	0.82	—	t—r	
8	T 167	1.50	0.89	—	t—r	
9	T 164	1.50	~0.89	—	t—r	
10	T 165	1.48	0.78	1.24	t—r	Figured on Pl. I, Figs. 1–2.
11	T 1	1.44	0.81	1.26	t—r	THORSLUND 1940, Pl. 1, Fig. 1.
12	T 233	1.37	0.79	—	t—r	
13	T 174	1.27	0.69	—	t—l	
14	T 168	1.03	0.56	—	t—r	

The width (tr.) of the frill along the mid-length of the valve is about $^{2}/_{3}$–$^{5}/_{8}$ of the height (tr.) of the lateral surface of the domicilium. The dorsal ends of the frill are straight and lie more or less at the same line as the dorsal margin of the valve (cf. THORSLUND 1940, Pl. 1, Fig. 1).

Compared with the length of the lateral surface of the domicilium the dolon of *C. sudermannica* is apparently slightly shorter (long.) than in *C. dentifera*. The available material is, however, too small and partly too fragmentary for the definition of this difference. A narrow proximal part of the dolon adjacent to the domicilium is almost smooth to faintly striate, the other parts of the dolon being ornamented by relatively large, closely spaced tubercles of somewhat irregular shape.

DIMENSIONS.—See Table 1.

DISCUSSION.—*Chilobolbina sudermannica* resembles rather much *C. dentifera*, but differs from it amongst others by the following characters: (1) the reticulation of the lateral surface of the domicilium is much coarser, and covers the whole surface; (2) the tubercles on the dolon are larger, and the radial striation of the proximal part of the dolon is much fainter to almost absent; (3) the heteromorphs attain a larger size; (4) the frill seems to be thicker and more solidly built. These differences are so constant in the material studied that the present writer proposes these two forms be regarded as two separate species.

OCCURRENCE.—*Chilobolbina sudermannica* n.sp. has been found up to now only in erratic boulders at Ringsö, Tvären area, Södermanland. Lower part of the *Ludibundus* limestone.

Chilobolbina lativelata n.sp.

Pl. I, Figs. 8–11.

? *1924 Chilobolbina dentifera* (Bonn.) sp.—Kummerow, p. 441 (listed only).

Holotype.—Right heteromorphic valve (SGU), figured on Pl. I, Figs. 10–11.

Type Locality.—Östergötland, Motala bore.

Type Stratum.—*Schroeteri* limestone, at the level of 111.63 m of the core.

Diagnosis.—Length of the lateral surface of the heteromorphs 1.25–1.45 mm. The whole lateral surface ornamented by a distinct, rather fine reticulation. The whole external surface of the dolon radially striated. The dorsal ends of the frill extend beyond the dorsal margin of the valve.

Specific Characters.—Outline and convexity on the whole as in *C. dentifera*. The adductorial pit is of somewhat varying size, but usually slightly smaller than in other species of *Chilobolbina*. On comparison with the other species of this genus no difference in the shape, number, or arrangement of the denticles on the inner side of the pit could be observed.

The whole lateral surface of the domicilium except the area dorsally of the adductorial pit and, occasionally at least, also a narrow area adjacent to the outer margin of the surface ornamented by a distinct, fine reticulation, clearly finer than that in *C. sudermannica*. The ornamentation includes also scattered tubercles, preponderantly on the ventral part of the lateral surface and close to the dorsal margin of the valve where they are usually arranged in an irregular row.

Velar frill moderately thick, its width (tr.) along the mid-length of the valve about $^{3}/_{5}$–$^{5}/_{7}$ of the height of the lateral surface of the domicilium. Dorsal ends of the velar frill pointed, extending considerably beyond the dorsal margin of the valve (cf. Pl. I, Fig. 8). In lateral direction the distal part of the frill seems to extend less than in other species of *Chilobolbina*, the whole frill being directed more ventrally.

In *C. lativelata* the dolon is comparatively longer and broader than in other species of *Chilobolbina*, its axial length being about $^{7}/_{10}$–$^{8}/_{11}$ of the length of the lateral surface of the domicilium. In *C. sudermannica* the same ratio is about $^{3}/_{5}$. The whole external surface of the dolon is radially striated and without tubercles.

Dimensions.—See Table 2.

Discussion.—*Chilobolbina lativelata* n.sp. differs from other species of *Chilobolbina* mainly by the ornamentation of the dolon and of the lateral surface of the domicilium, and by the comparatively small size of the heteromorphs. As this species is the earliest species of *Chilobolbina* known so far it is interesting to note that its dolon is relatively the longest, occupying in this respect an intermediate position between *Laccochilina* and the other species of *Chilobolbina*.

Table 2.

No.	Mus. cat. no.	L. domic.	H. domic.	H-L	Valve	Locality	Remarks
1	SGU	~1.45	0.85	—	h—r	Motala 111.63 m	Holotype. Pl. 1, Figs. 10–11.
2	,,	1.34	0.80	—	h—l	Motala 116.14 m	
3	,,	1.25	0.76	—	h—l	Motala 116.10 m	
4	,,	1.17	0.74	0.99	t—r	Motala 116.20 m	Figured on Pl. I, Fig. 8.
5	,,	1.11	0.64	—	t—r	Skärlöv 2.80 m	
6	RM AR. 19683	1.32	~0.73	1.15	h—r	Öl., between Lerkaka village and the beach.	Figured on Pl. I, Fig. 9.

OCCURRENCE.—*C. lativelata* n.sp. occurs in the *Platyurus* and *Schroeteri* limestones.

Östergötland.—Motala bore (6 heterom., 10 tecnom.); Smedsby Gård bore (1 tecnom.). *Öland.*—Skärlöv bore (1 heterom., 1 tecnom.); Gammalsby bore (2 tecnom.); exposure between Lerkaka village and the beach (RM, coll. J. G. ANDERSSON 1892, figured on Pl. I, Fig. 9; this specimen, mentioned also by THORSLUND 1940, p. 167, is evidently derived from the grey *Schroeteri* limestone and not from *Chasmops* beds as suggested by THORSLUND).

Gen. *Laccochilina* HESSLAND, 1949

TYPE SPECIES.—*Eurychilina estonula* ÖPIK, 1935.

DIAGNOSIS.—Unisulcate, with a well-defined adductorial pit. Tecnomorphs with a moderately broad concave velar frill of more or less uniform width along its whole extension; heteromorphs with the anteroventral and ventral parts of the frill inflated forming a well-defined, strongly convex dolon. The velar structure may be entire or represented posteriorly by a row of spines.

DISCUSSION.—The eurychilinids from the Lower *Vaginatum* limestone of the Siljan district were placed by HESSLAND (1949) into the genera *Eurychilina* and *Laccochilina*. HENNINGSMOEN (1953a, p. 228) pointed out that the dolon of the American species of *Eurychilina* has a construction which differs from that of the European species placed into this genus. According to him the species assigned by HESSLAND to *Eurychilina* can be transferred to *Laccochilina* since "there seems to be an even transition of forms from these species [assigned to *Eurychilina*] to the type species of *Laccochilina*" (HENNINGSMOEN 1953a, p. 228). After a careful examination of HESSLAND's original material this suggestion of HENNINGSMOEN is adopted provisionally in the present paper.

As pointed out by THORSLUND (1940, p. 166) the egg-shaped velar pouch (= dolon) in *Chilobolbina* can be derived through posterior and anterior constriction of the dolon, and there are thus no essential differences in the construction of the dolon between this genus and the species included here in

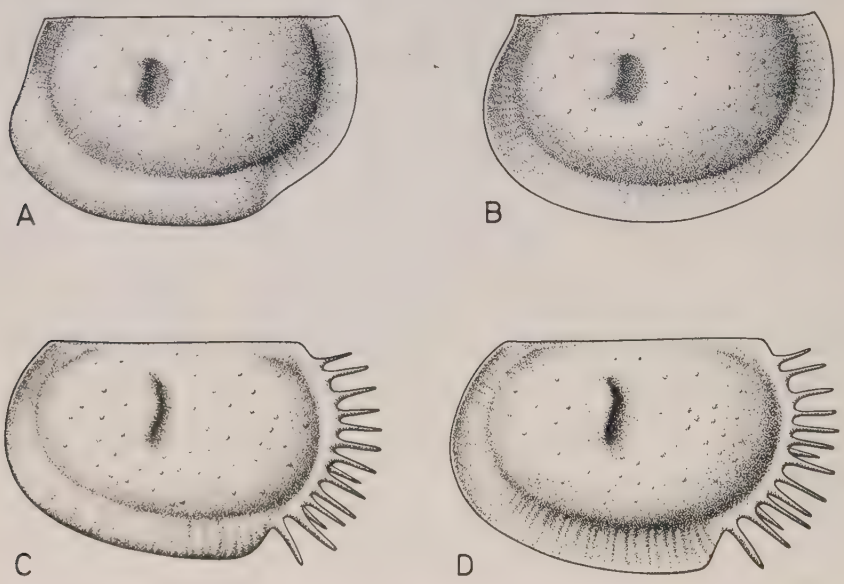


Fig. 14. Reconstructions (A, B) of *Laccochilina* (*Laccochilina*), mainly after *L.* (*L.*) *paucigranosa* n.sp., and (C, D) of *Laccochilina* (*Prochilina*) *decumana* (Bonnema). To the left heteromorphs (A, C), to the right tecnomorphs (B, D).

Laccochilina. *Laccochilina* differs from *Chilobolbina* by the narrower frill, the longer dolon, absence of the denticles in the adductorial pit, coarser partitions of the frill, and by the convexity of the lateral surface of the domicilium. In spite of these differences *Laccochilina* is apparently closely related to *Chilobolbina*.

Coelochilina is a peculiar genus since, according to Ulrich (1890, p. 129), the velar frill of its type species is always convex. If this be true, the taxonomic position of this genus is so far uncertain. If, on the other hand, the specimens described by him are heteromorphic, this genus differs from *Laccochilina* by the dolon being formed along the whole extension of the frill. A re-examination of the type species of *Coelochilina* is badly needed. *Apatochilina* differs from *Laccochilina* by being almost non-sulcate. Only tecnomorphs of this genus have been described so far.

In respect to the development of the velar structure two distinct groups of species can at present be distinguished within the genus *Laccochilina*. In the first group the velar structure is entire, reaching posteriorly up to the posterior cardinal corner without any considerable decrease in its width. This group includes the type species of *Laccochilina*, and is treated in the present paper as a separate subgenus *Laccochilina* (*Laccochilina*). In the second group the velar structure is developed posteriorly as a row of spines, and may be regarded as a specialized off-shoot from the first group. As the material studied has shown the posteriorly spinose species of *Laccochilina* to form a well-defined

group they are separated as a new subgenus *Laccochilina* (*Prochilina*). Both subgenera resemble each other closely in the relative width of the frill, the shape and length of the dolon, and the coarseness of the partitions within the frill. For this reason the present writer prefers to regard for the time being these groups as subgenera of one genus, and not as separate genera.

Occurrence.—The genus *Laccochilina* appears in the Arenig ($B_{II}\beta$ of Estonia), and continues apparently throughout the whole Ordovician. It is known so far only from Baltoscandia.

Subgen. *Laccochilina (Laccochilina)* Hessland, 1949

Text-fig. 14A, B.

Subgenotype.—*Eurychilina estonula* Öpik, 1935.

Diagnosis.—Velar frill reaching posteriorly up to the posterior cardinal corner without any considerable decrease in its width. Preadductorial node comparatively prominent.

Species.—*Eurychilina estonula* Öpik, 1935
Eurychilina dorsotuberculata Hessland, 1949
Eurychilina rugosotuberculata Hessland, 1949
Laccochilina centrotuberculata Hessland, 1949
? *Laccochilina densituberculata* Hessland, 1949
Laccochilina levis Hessland, 1949
? *Laccochilina dorsoplicata* Hessland, 1949
? *Laccochilina tarda* Henningsmoen, 1954
Laccochilina (*Laccochilina*) *paucigranosa* n. sp.
Laccochilina (*Laccochilina*) *bulbata* n. sp.

Chilobolbina dimorpha Thorslund, 1948, has been erected on internal moulds and is not determinable at the specific level (nomen dubium, cf. p. 246). Also *Primitia Schmidtii* Krause, 1889, is evidently a species of *Laccochilina* (*Laccochilina*), but in case the type material be lost it should be considered as a nomen dubium.

Discussion.—The type species of *Laccochilina*, *L.* (*L.*) *estonula*, is poorly known so far. Öpik (1935, Pl. I, Figs. 6, 7) figured two somewhat fragmentary heteromorphic valves, and a tecnomorphic valve from the type locality has been studied by the present writer. This species lacks the dorsal ridge, the deep adductorial pit is rounded, and there exists also a rather distinct sulcal depression dorsally of the pit. The rather low preadductorial node is distinctly delimited dorsally and posteriorly, merging ventrally and anteriorly into the general surface of the preadductorial area with only a slight change in convexity. The Text-fig. 3 in Öpik (1935, p. 8) is apparently intended to show only the location of the node and of the adductorial pit both of which are in

reality much less distinct. The reconstruction of this species attempted by Kesling (1951c, Pl. III, Fig. 4) after the figures published by Öpik (1935) also gives an erroneous impression with regard to the adductorial pit and the preadductorial node. The surface of the valve is distinctly, finely reticulate in *L.* (*L.*) *estonula*, but on its ventral part the ornamentation seems to include also fine granules. Possibly it is both granulose and reticulate.

It is often difficult to arrive at a specific determination of *Laccochilina* (*Laccochilina*) specimens as the different species may evidently have a closely similar general appearance. The best specific characters of the species studied seem to lie in the ornamentation, the outline of the adductorial pit, and the shape of the dolon. The specimens in which surface corrosion or disintegration prevents the observation of these details are hardly determinable specifically. Unfortunately also in the material studied the state of preservation is often rather poor, and there remains, therefore, some uncertainty concerning the degree of the individual variation of the tuberculate ornamentation and of the shape of the dolon.

Laccochilina (*Laccochilina*) as defined in the present paper includes for certain morphological characters a wide range of variation. It is probable that a close study of certain Upper and Lower Ordovician species may necessitate their removal into separate subgenera or even genera. A general revision of the species of *Laccochilina* lies, however, outside the scope of the present paper.

Occurrence.—The vertical and horizontal distribution of this subgenus coincides on the whole with that of the genus.

Laccochilina (Laccochilina) paucigranosa n. sp.

Pl. I, Figs. 12–17; Text-fig. 11C.

? 1948 *Chilobolbina dimorpha* n. sp.—Thorslund, p. 366, Text-fig. 6, Pl. XX, Fig. 14.

Holotype.—Left heteromorphic valve UM no. B 287, figured on Pl. I, Figs. 16–17.

Type Region.—South Bothnian area. No type locality as the holotype was found in an erratic boulder at Erken, Upland.

Type Stratum.—*Crassicauda* limestone.

Derivation of the Name.—From Lat. *paucus* = few + *granum*, referring to the ornamentation consisting of a few distinct tubercles.

Diagnosis.—Length of the lateral surface of the heteromorphs 1.20–1.30 mm. Adductorial pit oblong, comparatively large, preadductorial node distinct, with poorly defined anterior boundary. Surface of the valve as a rule with distinct depressions posterodorsally of the adductorial pit and anterodorsally of the preadductorial node. No distinct trace of a dorsal plica. Lateral surface of the domicilium and that of the dolon ornamented with a small number of scattered tubercles, most of them of about equal size.

Description.—Postadductorial area of the valve comparatively strongly convex, preadductorial area rather evenly sloping from the preadductorial node forwards (cf. Pl. I, Fig. 17). Summit of the valve slightly behind the preadductorial pit. Dorsum comparatively high, flattened, epicline. No clear trace of a dorsal ridge.

Preadductorial pit rather large, oblong, somewhat kidney-shaped with more or less straight or slightly concave anterior, and strongly convex posterior margin, situated about halfway between the velum and the hinge-line. Lateral surface of the domicilium as a rule with a distinct shallow depression posterodorsally from the pit and a similar but fainter depression anterodorsally from the preadductorial node. Between these depressions the surface of the valve is slightly elevated, forming a rather distinct dorsal boundary of the adductorial pit. The ventral end of the pit is mostly surrounded by a low, ridge-like elevation. Preadductorial node comparatively low with a distinct posterior margin; anteriorly the surface of the node merges more or less smoothly into the general surface of the preadductorial area. Occasionally a distinct node can be observed near the anterior corner of the valve.

Tecnomorphs with a broad concave frill, more or less uniform in width, and with a faintly undulate surface. The internal partitions comparatively coarse and well-defined. Heteromorphs with a strongly convex dolon. The lateral surface of the dolon is moderately convex, its boundary against the domicilium marked by a wide, shallow furrow, the ventral surface sloping almost vertically in lateral view (Pl. I, Figs. 14, 17; Text-fig. 11C). The posterior end of the dolon is as a rule situated at the mid-length of the postadductorial area or slightly behind it. The whole surface of the dolon is radially striated. According to one more or less complete heteromorphic carapace the peripheral margins of the dolon are in contact in closed carapaces. The subvelar field was not accessible for observation.

The ornamentation consists of a small number (25–45, excl. of frill) of usually rather distinct, widely scattered tubercles which form an irregular row near the dorsal margin. Most of the tubercles are comparatively large and of about uniform size; here and there, however, also smaller granules occur. The surface of the valve between the granules appears to be smooth. Scattered large tubercles occur also on the lateral surface of the dolon. In one specimen of Furudal, Siljan district (Pl. I, Fig. 13), the surface of the valve between the large tubercles is finely granulate, otherwise this specimen does not exhibit any conspicuous differences compared with those from the South Bothnian area.

Dimensions.—See Table 3. All specimens measured have been found in the South Bothnian erratic boulder Erken no. 10.

Discussion.—It is possible that *L.* (*L.*) *paucigranosa* n.sp. is conspecific with *Chilobolbina dimorpha* Thorslund, 1948, but this cannot be proved. The holotype of *L.* (*L.*) *dimorpha* is an internal mould of a young tecnomorphic

Table 3.

No.	UM Mus. cat. no.	L. domic.	H. domic.	H. valve	H-L	Valve	Remarks
1	B 288	1.28	0.71	0.93	—	h—l	
2	B 286	1.26	0.69	0.95	—	h—l	Figured on Pl. I, Fig. 12.
3	B 294	1.23	0.67	0.91	1.19	h—l	
4	B 287	1.23	0.66	0.87	—	h—r	Holotype. Pl. I, Figs. 16–17.
5	B 292	1.21	0.64	0.87	—	h—r	
6	B 291	1.20	0.64	0.87	—	h—r	
7	B 293	1.06	0.61	—	—	t—l	
8	B 290	0.92	0.52	—	—	t—r	
9	B 289	0.76	0.43	—	—	t—r	

valve (Thorslund 1948, Pl. XX, Fig. 14) which is not determinable specifically. Also the heteromorphic valve figured by Thorslund (1948, p. 366, Text-fig. 6) is too poorly preserved to allow of specific determination. In the *Crassicauda* limestone of the Kullatorp and Norra Skagen bores, Kinnekulle, specimens of *Laccochilina* (*Laccochilina*) are occasionally fairly common, but practically all of them are preserved as internal moulds and are, therefore, specifically indeterminable. In the Stora Åsbotorp bore several well-preserved specimens of *L.* (*Laccochilina*) have been encountered roughly on the same level as the holotype of *L.* (*L.*) *dimorpha*, but these specimens differ in several respects from *L.* (*L.*) *paucigranosa*. They probably belong to a new species which, however, cannot be defined until more material is available [cf. *L.* (*L.*) sp. A., below]. Since the type specimens of *L.* (*L.*) *dimorpha* are specifically indeterminable this species is better regarded as a nomen dubium.

Laccochilina (*L.*) *paucigranosa* differs from the other hitherto described species of this subgenus without a dorsal plica by the combination of characters given in the diagnosis.

Occurrence.—The species described has hitherto been found only in the *Crassicauda* limestone.

South Bothnian area.—Erratic boulder Erken no. 10 (7 heterom, 6 tecnom.). *Siljan district.*—Furudal, the quarry at the rivulet Kalkbergsbäcken (4 heterom., 4 tecnom.). *Östergötland.*—Motala bore (1 heterom.); Smedsby Gård bore (1 heterom., 4 tecnom.).

Laccochilina (Laccochilina) sp. A

Pl. II, Fig. 1.

Specimens of *Laccochilina* (*Laccochilina*) from the *Crassicauda* limestone of the Stora Åsbotorp bore differ in several respects from those of *L.* (*L.*) *paucigranosa*. Their adductorial pit is somewhat larger and deeper, and has a more

rounded outline than that of the latter species. The dolon is wider (tr.) and shorter, as a rule not reaching the mid-length of the postadductorial area. The ornamentation is on the whole identical with that of *L.* (*L.*) *paucigranosa*, but the tubercles are usually missing on the dolon and fewer in number on the lateral surface of the domicilium. The length of the domicilium of the heteromorphs agrees on the whole with that of *L.* (*L.*) *paucigranosa*. These specimens probably belong to a new species which, however, cannot be properly defined until more material is available.

Occurrence.—*Crassicauda* limestone. *Västergötland.*—Billingen, Stora Åsbotorp bore (3 heterom., 3 tecnom.). *Östergötland.*—Smedsby Gård bore (1 tecnom.).

Laccochilina (Laccochilina) sp. B

Pl. II, Figs. 2–4.

Specimens of *Laccochilina* (*Laccochilina*) from the South Bothnian erratic boulder Bergsbrunna no. 1 resemble on the whole *L.* (*L.*) *paucigranosa*, but differ from it by the following characters: (1) the heteromorphs are slightly smaller; (2) the dolon seems to be comparatively broader (tr.); (3) the ornamentation consists of rather small, closely spaced granules; the diameter of the granules exceeds as a rule considerably the interstices. In addition to the granules also a small number of scattered tubercles of the same size as in *L.* (*L.*) *paucigranosa* occurs on the lateral surface of the domicilium and on that of the dolon. The differences in the ornamentation suggest that these specimens may belong to a new species, but as the material available is small and comparatively poorly preserved it is difficult at present to give of this species a proper definition.

Occurrence.—Uppermost *Crassicauda* limestone. South Bothnian area, erratic boulder Bergsbrunna no. 1 (3 heterom., 6 tecnom.).

Laccochilina (Laccochilina) sp. C

Pl. II, Figs. 5–8.

1940 *Chilobolbina* cf. *kuckersiana* (Bonnema)—Thorslund, pp. 168—169, Pl. 3, Fig. 11.

The specimens of *Laccochilina* (*Laccochilina*) from the Tvären area differ from *L.* (*L.*) *paucigranosa* by the following characters: (1) the heteromorphs attain a much larger size (1.40–1.50 mm); (2) the preadductorial node seems as a rule to be slightly smaller; (3) the depressions posterodorsally of the adductorial pit and anterodorsally of the preadductorial node are fairly indistinct. The ornamentation varies rather considerably in the specimens studied. In some large specimens the central part of the lateral surface of the domicilium is ornamented by minute granules of slightly varying size and by a small number (30–40) of larger tubercles of a more uniform size (Pl. II, Fig. 6). In

Table 4.

No.	UM Mus. cat. no.	L. domic.	H. domic.	H. valve	Valve	Remarks
1	T 260	1.48	0.81	1.10	h—l	Figured on Pl. II, Figs. 7–8.
2	T 29	1.40	0.78	1.03	h—r	Pl. II, Fig. 6; Thorslund 1940, Pl. 3, Fig. 11.
3	T 261	1.21	0.66	—	t—r	Figured on Pl. II, Fig. 5.
4	T 262	1.17	0.67	—	t—r	

other specimens the small granules are hardly perceptible to absent (cf. Pl. II, Fig. 8), and in small specimens only a small number of large tubercles is present (Pl. II, Fig. 5). A distinctive feature of all these specimens is the complete absence of any ornamentation on the outer part of the lateral surface of the domicilium, the sudden change in ornamentation rendering the boundary between the central and outer part of this surface quite distinct.

Also these specimens probably belong to a new species but the material is at present insufficient for the establishment of a clear definition of this species.

Dimensions.—See Table 4.

Occurrence.—Lowermost *Ludibundus* beds. Södermanland, Tvären area, Ringsö, erratic boulders (2 heterom., 4 tecnom.).

Laccochilina (Laccochilina) bulbata n. sp.

Pl. II, Figs. 9–14.

Holotype.—Left heteromorphic valve (SGU), figured on Pl. II, Fig. 14.

Type Locality.—Östergötland, Motala bore.

Type Stratum.—*Platyurus* limestone, at the level of 114.10 m of the bore.

Derivation of the Name.—From Lat. *bulbus*, referring to the prominent preadductorial node.

Diagnosis.—Length of the lateral surface of the heteromorphs 1.40–1.50 mm. Adductorial pit oblong, fairly large, preadductorial node prominent, but with a rather indistinct anterior boundary. A distinct dorsal plica close to the cardinal corner fields. Surface of the frill strongly undulate. Lateral surface of the domicilium ornamented by large scattered tubercles and minute closely spaced granules.

Description.—Highest convexity of the valve slightly behind the adductorial pit, the top of the preadductorial node being as a rule lower than the summit of the valve. Dorsum rather high, epicline, highest (tr.) close to the cardinal corners, at the point where the dorsal plica reaches the dorsal margin.

Adductorial pit comparatively narrow, kidney-shaped, distinctly defined except dorsally. Surface of the valve slightly depressed dorsally of the pit.

Table 5.

No.	Museum	L. domic.	H. domic.	H. valve	H-L	Valve	Locality	Remarks
1	SGU	1.50	0.91	1.17	—	h—r	Motala 111.89 m	
2	,,	1.48	0.90	1.16	—	h—r	,, 112.95 m	
3	,,	1.44	0.84	1.12	—	h—r	,, 112.06 m	Figured on Pl. II, Fig. 11.
4	,,	1.41	0.86	1.15	—	h—l	,, 114.10 m	Holotype. Pl. II, Fig. 14.
5	,,	1.46	0.88	—	1.26	t—l	,, 116.24 m	Figured on Pl. II, Fig. 12.
6	,,	1.26	0.77	—	—	t—r	,, 112.05 m	,, ,, Pl. II, Fig. 13.
7	,,	1.04	0.65	—	0.86	t—r	,, 119.17 m	,, ,, Pl. II, Fig. 9.
8	,,	1.42	0.82	1.09	—	h—l	Gammalsby 11.20 m	,, ,, Pl. II, Fig. 10.

Preadductorial node oblong, of slightly varying relative size, nearly about as long (tr.) as the pit to about $^2/_3$ of the length (tr.) of the pit. The anterior boundary of the node is usually poorly defined, being formed only by a slight change in convexity. Dorsal plica prominent forming two arches at the dorsal margin, one in front of and the other behind the adductorial pit. In the middle, at about the height of the adductorial pit the plica is almost completely obsolete, both of its arches being connected there by a low, poorly defined elevation.

The velar frill is moderately broad, with a strongly undulate surface, entire, reaching on both ends the cardinal corners, concave in tecnomorphs. Dolon strongly convex, broadest anteroventrally, its ventral surface almost vertical in lateral view (cf. Pl. II, Fig. 10). The posterior end of the dolon extends considerably behind the mid-length of the postadductorial area, the anterior end is situated at about the longitudinal line through the middle of the preadductorial pit.

The lateral surface of the valve ornamented by minute, closely spaced granules and large tubercles (Pl. II, Fig. 11). The frill is covered by a very fine concentric striation, and lacks tubercles. In a small specimen figured on Pl. II, Fig. 9 the larger tubercles are more widely spaced than in other specimens, but this difference is probably due to individual variation.

Dimensions.—See Table 5.

Discussion.—*Laccochilina* (*Laccochilina*) *bulbata* differs from other congeneric species with a dorsal plica mainly by its ornamentation, the strongly undulate surface of the frill, and the oblong, anteriorly comparatively poorly defined preadductorial node.

Occurrence.—The species described has been found in the *Platyurus* limestone and in Östergötland also in the lowermost part of the *Schroeteri* limestone.

Östergötland.—Motala bore (12 heterom., 26 tecnom.). *Siljan district.*—Fjäcka (1 heterom., 1 tecnom.). *Öland.*—Böda Hamn bore (1 tecnom.); Gammalsby bore (1 heterom., 1 tecnom.).

Subgen. *Laccochilina (Prochilina)* n. subgen.

Type Species.—*Primitia decumana* Bonnema, 1909.

Diagnosis.—Dorsal plica faint, obsolete in the middle. The posterior part of the velar structure developed as a row of spines.

Species.—*Primitia decumana* Bonnema, 1909, and *Laccochilina* (*Prochilina*) *ostrogothica* n. sp.

Discussion.—It is now apparent that the spinose development of the posterior part of the velar structure characterizes a well-defined group of species within the genus *Laccochilina*. For this group the new subgenus *Laccochilina* (*Prochilina*) is here proposed. In respect to other characters, especially to the shape of the dolon, *L.* (*Prochilina*) is closely similar to *Laccochilina* (*Laccochilina*). In the specimens of *L.* (*Prochilina*) studied a low dorsal ridge is almost invariably present near the cardinal corners, and this and the usually poor development of the preadductorial node may be regarded as additional characters of this subgenus.

Occurrence.—The species of the subgenus *Laccochilina* (*Prochilina*) hitherto known are restricted to the Middle Ordovician: the *Crassicauda* and *Ludibundus* limestones of Sweden, and the Uhaku and Kukruse Stages of Estonia.

Laccochilina (Prochilina) decumana (Bonnema, 1909)

Pl. II, Figs. 15–16; Pl. III, Figs. 1–4; Text-fig. 14C–D, 15.

1909 *Primitia decumana* n. sp.—Bonnema, pp. 26–27, Pl. II, Figs. 10–14.
1924 *Primitia decumana* Bonn.—Kummerow, p. 440 (*partim?*).
1934 *Eurychilina decumana* (Bonnema)—Bassler & Kellett, p. 314.
1937 *Eurychilina decumana* (Bonnema)—Öpik, p. 21 (*partim?*). ? Pl. XII, Fig. 8.
1940 *Chilobolbina decumana* (Bonnema)—Thorslund, p. 168, Pl. 3, Figs. 8–10, Text-fig. 57 (p. 166).
1955 *Laccochilina decumana* (Bonnema)—Sarv, p. 13 (*partim?*).
1956a *Laccochilina decumana* (Bonnema)—Sarv, p. 49 (*partim?*).

Lectotype.—Left heteromorphic valve, TM no. Os-2305, figured by Bonnema 1909, Pl. II, Figs. 13–14 (designated herein).

Type Locality.—Kukruse, Estonia.

Type Stratum.—Kohtla zone of the Kukruse Stage ($C_{II}\alpha$).

Diagnosis.—Length of the lateral surface of the heteromorphs 2.15–2.45 mm. Adductorial pit about 5 times longer (tr.) than broad, kidney-shaped, with a more or less uniform width, the transversal distance between the ventral end of the pit and the frill equal to the length (tr.) of the pit or slightly less. Lateral surface of the valve ornamented by minute granules of a diameter which is mostly somewhat larger than the space between the granules and by a number of large tubercles.

Description of the Specimens from the Tvären Area.—Valves in ventral view fairly regularly convex, greatest convexity as a rule slightly behind the

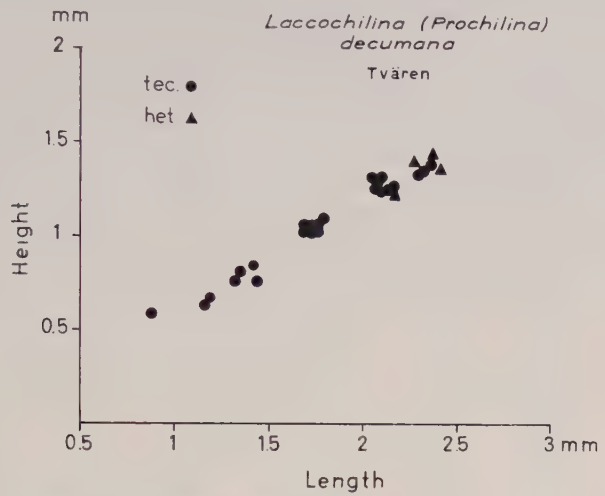


Fig. 15. Size dispersion of the valves of *Laccochilina* (*Prochilina*) *decumana* (BONNEMA) from the erratic boulders of the Tvären area. Length and height of the lateral surface of the domicilium are given. Triangles refer to the heteromorphs (*het.*), and dots to the tecnomorphs (*tec.*). The last three moult stages are rather well distinguished.

adductorial pit (cf. Pl. II, Fig. 16; Pl. III, Fig. 4). Dorsum comparatively low, almost orthocline to slightly epicline. Close to each cardinal corner a low, obliquely directed dorsal plica merging into the general surface of the valve towards the mid-length of the valve.

Adductorial pit rather long (tr.), narrow, kidney-shaped, with convex posterior and concave anterior margin, of almost uniform width. Length (tr.) of the pit exceeds its width in the middle about 5 times. The transversal distance between the ventral end of the pit and the frill only slightly shorter than the length of the pit; the transversal distance between the dorsal end of the pit and the dorsal margin of the valve slightly shorter than half the length of the pit. Surface of the valve in front of the middle of the adductorial pit slightly raised, forming a low and anteriorly poorly defined preadductorial node.

Anteriorly and anteroventrally the velar structure is developed as a moderately broad frill with a strongly undulate surface, concave in tecnomorphs (cf. Pl. III, Fig. 3). Posteriorly the frill reaches up to about the mid-length of the postadductorial area; behind this the velar structure is developed as a row of rather long, slender spines (Pl. III, Fig. 2) all of which do not, however, lie on exactly the same level. These spines are fully developed already on the smallest specimens examined (length of the lateral surface of the valve 0.88 mm; cf. also BONNEMA 1909, Pl. II, Fig. 11).

In heteromorphs almost the whole velar structure which in tecnomorphs is developed as a frill is swollen into a strongly convex dolon. Only close to the anterior cardinal corner dorsally from the mid-height of the domicilium the frill retains its tecnomorphic concave shape.

Table 6.

No.	UM Mus. cat. no.	L. domic.	H. domic.	H. valve	H-L	Valve	Remarks
1	T 250	2.41	1.35	1.71	1.89	h—l	Figured on Pl. II, Figs. 15–16.
2	T 28	2.37	1.43	1.75	1.84	h—r	Thorslund 1940, Pl. 3, Figs. 9–10.
3	T 257	2.24	1.39	1.67	—	h—l	
4	T 265	2.17	1.23	1.63	—	h—r	
5	T 241	2.36	1.39	—	1.81	t—l	Figured on Pl. III, Fig. 2.
6	T 240	2.32	1.35	—	—	t—l	
7	T 238	2.29	1.33	—	1.80	t—r	Figured on Pl. III, Fig. 1.
8	T 252	2.16	1.26	—	—	t—l	
9	T 236	2.13	1.25	—	1.59	t—r	
10	T 263	2.09	1.35	1.58	—	t—r	
11	T 248	2.08	1.31	—	—	t—l	
12	T 247	2.07	1.27	—	1.69	t—r	
13	T 254	2.06	1.30	—	—	t—l	
14	T 27	2.06	1.26	—	—	t—r	Thorslund 1940, Pl. 3, Fig. 8.
15	T 251	1.79	1.10	—	—	t—l	
16	T 243	1.76	1.07	—	—	t—r	Figured on Pl. III, Fig. 3.
17	T 245	1.74	1.04	—	—	t—r	
18	T 244	1.73	1.04	—	1.32	t—r	
19	T 264	1.72	1.05	—	—	t—l	
20	T 239	1.72	1.02	—	—	t—r	
21	T 237	1.69	1.06	—	—	t—l	
22	T 242	1.69	1.05	—	—	t—r	
23	T 246	1.42	0.76	—	—	t—l	
24	T 258	1.41	0.85	~1.04	—	t—r	
25	T 253	1.35	0.81	—	—	t—l	
26	T 256	1.32	0.76	—	—	t—l	
27	T 259	1.18	0.68	—	—	t—r	
28	T 249	1.16	0.63	—	—	t—r	
29	T 255	0.88	0.59	—	—	t—r	

Subvelar field (Pl. III, Fig. 4) low (tr.), concave. Both valves with a row of coarse marginal tubercles.

The lateral surface of the valve is ornamented by small, closely spaced granules, the diameter of which is commonly somewhat larger, but occasionally also equal to, or smaller than, the space between the granules. A small number of large tubercles are scattered between the granules. In specimens with a corroded or otherwise worn surface the granules can as a rule not be observed, and the ornamentation is formed by the tubercles only. The areas postero- and anterodorsally of the dorsal ridge are smooth. In well-preserved specimens the velar frill is very finely concentrically striate and ornamented with a small number of tubercles.

Dimensions.—See Table 6. All specimens measured have been found in erratic boulders of the Tvären area, Södermanland.

Discussion.—This relatively large species is easily distinguished by the shape of the adductorial pit and by the ornamentation. It is uncertain at present whether the small tecnomorphic valve from the Uhaku Stage of Estonia figured by Öpik (1937, Pl. XII, Fig. 8) really belongs to *L.* (*P.*) *decumana*. Full certainty as to the identity of this specimen can be obtained first when heteromorphs of *Laccochilina* (*Prochilina*) have been found in the same beds (cf. also p. 254).

Occurrence.—*Laccochilina* (*Prochilina*) *decumana* seems to be restricted to the lower and middle part of the *Ludibundus* limestone of Sweden and the contemporaneous beds of Estonia ($C_{II}\alpha$).

Estonia.—Kukruse. *Södermanland*, Tvären area.—Ringsö (boulders) (7 heterom., 35 tecnom.). *Östergötland*.—Smedsby Gård bore (2 tecnom.); the specimen from Karstorp, parish of Lönsås, mentioned by Thorslund (1940, p. 168; an internal mould of a tecnomorphic valve, UM) was found to be specifically indeterminable. *Jämtland*, Brunflo-Lockne area.—Cf. Thorslund 1940, p. 49.

Laccochilina (Prochilina) ostrogothica n. sp.

Pl. III, Figs. 5–8.

? *Eurychilina decumana* (Bonnema)—Öpik, Pl. XII, Fig. 8.

Holotype.—Right heteromorphic valve (SGU), figured on Pl. III, Figs. 7–8.

Type Locality.—Östergötland, Motala bore.

Type Stratum.—Lowermost *Crassicauda* limestone, at the level of 105.57 m of the bore.

Derivation of the Name.—After Östergötland, the province in which the type locality is situated.

Diagnosis.—Length of the lateral surface of the heteromorphs 1.50–1.65 mm. Adductorial pit comparatively broad (long.), about twice to thrice as long as broad, the transversal distance between the ventral end of the pit and the frill slightly larger than the length (tr.) of the pit. Ornamentation on the whole as in *L.* (*P.*) *decumana*.

Specific Characters.—Outline and convexity of the valve, and shape of the dorsal plica similar to those in *L.* (*P.*) *decumana*. Adductorial pit comparatively broad, about twice to thrice as long (tr.) as broad, slightly increasing in width dorsally, kidney-shaped, with convex posterior and concave anterior margin. The transversal distance between the ventral end of the pit and the frill slightly longer than the length (tr.) of the pit; the distance between the dorsal end of the pit and the dorsal margin of the valve about $^2/_3$ of the length of the pit. The surface of the valve in front of the pit is considerably elevated to form a preadductorial node which is more prominent than that of *L.* (*P.*) *decumana*.

Table 7.

No.	Mus. cat. no.	L. domic.	H. domic.	H. valve	Valve	Locality	Remarks
1	UM B 299	1.63	0.94	1.18	h—r	Boulder Erken no. 10	Figured on Pl. III, Fig. 6.
2	SGU	1.51	0.88	1.16	h—r	Motala 105.57 m	Holotype. Pl. III, Figs. 7–8.
3	,,	1.32	0.82	1.01	t—l	Motala 101.76 m	Figured on Pl. III, Fig. 5.

In anterior direction the surface of the node merges smoothly into the general surface of the preadductorial area.

Velar structure on the whole identical with that of *L.* (*P.*) *decumana*, the posterior spines seem, however, to be slenderer.

Ornamentation of the lateral surface of the domicilium on the whole as in *L.* (*P.*) *decumana*.

Dimensions.—See Table 7.

Discussion.—*Laccochilina* (*Prochilina*) *ostrogothica* differs from *L.* (*P.*) *decumana* by the smaller size of the heteromorphs, different size and shape of the adductorial pit, and by a more prominent preadductorial node.

The specimen from the Uhaku Stage of Estonia figured by Öpik (1937, Pl. XII, Fig. 8) as *Eurychilina decumana* may represent the species described. The adductorial pit is, however, slightly narrower than that of the specimens of *L.* (*P.*) *ostrogothica* examined, and the ornamentation consists, as far as can be judged after Öpik's figure, in addition to tubercles of minute very closely spaced granules. Such a kind of granulation has not been observed in any Swedish specimen of *L.* (*Prochilina*). On account of these differences more material of *L.* (*Prochilina*) from the Uhaku Stage must be examined before the species of this subgenus occurring in these beds can be determined.

Occurrence.—*L.* (*Prochilina*) *ostrogothica* has hitherto been found only in the *Crassicauda* limestone.

Östergötland.—Motala bore (1 heterom., 3 tecnom.); Smedsby Gård bore (3 tecnom.). *South Bothnian area.*—Erratic boulders Erken no. 10 (1 heterom.) and Bergsbrunna no. 1 (1 tecnom.).

Gen. *Cystomatochilina* n. gen.

Text-fig. 16.

Type Species.—*Primitia* (*Ulrichia?*) *umbonata* Krause, 1892.

Derivation of the Name.—From Greek κύρτωμα = node + diminutive of χεῖλος, referring to the prominent preadductorial knob in the type species.

Diagnosis.—Nearly non-sulcate or with a faint to fairly distinct, poorly defined adductorial pit. Preadductorial node prominent, knob-shaped in the

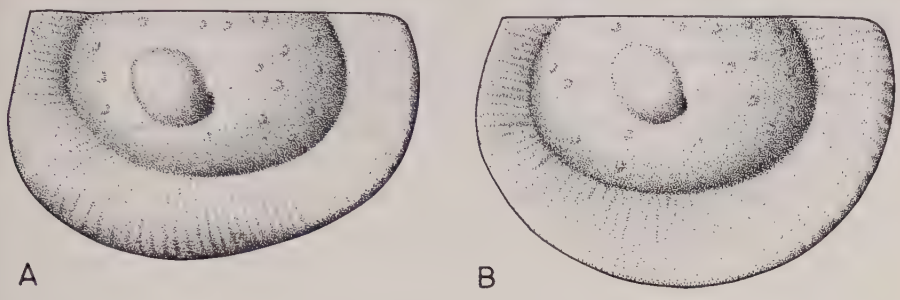


Fig. 16. Reconstruction of a heteromorph (A) and a tecnomorph (B) of *Cystomatochilina umbonata* (KRAUSE). Heteromorph after the specimen UM no. F 10 (MARTINSSON 1956a, Pl. I, Fig. 4), tecnomorph mainly after the specimen UM no. F 11 (MARTINSSON 1956a, Pl. I, Fig. 5).

type species. No dorsal plica. Tecnomorphs with a very wide frill, concave anteriorly and ventrally, faintly convex posteriorly, extending from one cardinal corner to the other. Heteromorphs ventrally and anteroventrally with a convex, broad (tr.) dolon.

SPECIES.—*Primitia* (*Ulrichia*?) *umbonata* KRAUSE, 1892
Platybolbina tiara HENNINGSMOEN, 1954
? *Platybolbina tiara densistriata* HENNINGSMOEN, 1954

DISCUSSION.—The type species was included by HENNINGSMOEN (1954b) in *Platybolbina*, but as it possesses a wide frill extending from one cardinal corner to the other this species cannot possibly belong to *Platybolbina*. All the numerous species of the latter genus have a characteristic extension of the velum (cf. for instance Fig. 18) which differs in this respect clearly from that of *C. umbonata*.

The lectotype of *C. umbonata* (designated by HENNINGSMOEN 1954b, p. 91) was refigured by TRIEBEL (1941, Pl. 4, Fig. 12). The heteromorph of this or of a very closely related species was depicted by MARTINSSON (1956a, Pl. I, Fig. 4; not Pl. I, Fig. 3, cf. MARTINSSON 1956b, p. 40).

Cystomatochilina is probably closely related to *Laccochilina*, and may be a late specialized off-shoot from the latter genus. The chief differences between these genera lie in the size of the adductorial pit, and in the width and shape of the frill. In the shape of the frill *Cystomatochilina* reminds of *Chilobolbina* which also in both dimorphs has a wide and posteriorly convex frill. In the former genus, however, the partitions within the velum are coarser, and the dolon is of quite a different shape.

Cystomatochilina tiara is on the whole similar to the type species, but differs from it by a larger adductorial pit, much lower and comparatively ill defined preadductorial node, and evidently coarser partitions within the velum. The inclusion of this species in *Cystomatochilina* is at present somewhat provisional. The same applies also to the Silurian *C. tiara densistriata*, but as only tecno-

morphs are known so far its generic reference is even more uncertain. Both these species exhibit, however, apparently greater similarity to the type species of *Cystomatochilina* than to any other eurychilinid genus.

Occurrence.—Upper Ordovician—? Silurian. Baltoscandia.

Actinochilina n. gen.

Type Species.—*Eurychilina suecica* Thorslund, 1948.

Derivation of the Name.—From Greek ἀκτίς = ray + diminutive of χεῖλος = lip, referring to the distinct partitions within the velum.

Diagnosis.—Unisulcate, sulcus deep, straight, more or less transversally directed, reaching to about half the height of the lateral surface of the domicilium, or slightly longer (tr.). Velar frill comparatively broad anteriorly and ventrally, narrowing considerably in posterodorsal and anterodorsal direction, and reaching the cardinal corners as a narrow flange or ridge; the decrease in width of the frill is as a rule stronger towards the posterior than towards the anterior cardinal corner. Frill of the tecnomorphs concave ventrally and posteroventrally and faintly convex anteroventrally; heteromorphs with a convex dolon anteroventrally and ventrally.

Species.—In addition to the type species another species is described in the present paper as *Actinochilina* sp. A.

Discussion.—The sulcation of *Actinochilina* is identical with that of *Eurychilina*, and the tecnomorphs of these genera seem to differ mainly by the outline of the frill. In the former genus the frill decreases considerably in width towards the cardinal corners, and in some species does not seem to reach the posterior cardinal corner (cf. Pl. III, Figs. 11–12), whereas in *Eurychilina* the frill is of about uniform width along its whole extension (cf. for instance Ulrich 1897, Pl. XLIV, Figs. 1, 2). The construction of the dolon is, however, widely different in these two genera, and the similarity of their sulcation is, therefore, apparently due to homoeomorphic development. In *Actinochilina* the shape of the dolon as far as known resembles that of *Cystomatochilina* and *Laccochilina*. From these genera the former genus differs by the shape of the sulcus and also by the considerable decrease in the width of the frill towards the cardinal corners.

Occurrence.—Middle Ordovician (Llandeilo, Lower Caradoc), Scandinavia.

Actinochilina suecica (Thorslund, 1948)

Pl. III, Fig. 9.

1948 *Eurychilina suecica* n. sp.—Thorslund, p. 368, Pl. XX, Figs. 8–9.
cf. *1953 Eurychilina suecica* Thorsl.—Lindström, pp. 128–130.
? *1953b Primitia suecica* (Thorslund)—Henningsmoen, pp. 49–50, Pl. 1, Fig. 14, Pl. 5, Fig. 7.

HOLOTYPE.—Right tecnomorphic valve, UM no. Vg 20, figured on Pl. III, Fig. 9; THORSLUND 1948, Pl. XX, Fig. 8.

TYPE LOCALITY.—Västergötland, Kinnekulle, Kullatorp bore.

TYPE STRATUM.—*Ludibundus* beds, at the level of 77.50 m of the core.

DESCRIPTION.—The type species being the only species hitherto described, its diagnosis coincides largely with that of the genus. All available material is moreover poorly preserved, and several taxonomically important details as the ornamentation and the details of the shape of the velar structure are therefore imperfectly known at present.

Domicilial outline slightly postplete, dorsum low, almost orthocline. Lateral surface of the domicilium relatively weakly and uniformly convex. Highest convexity of the valve at the preadductorial node which lies at about the same level as the surface surrounding the ventral end of the sulcus.

Sulcus deep, straight, transversally directed, slightly constricted in the middle, anterior end somewhat expanded. Preadductorial node flattened, low, poorly defined.

Velar frill rather wide, lateroventrally directed, in tecnomorphs slightly concave to almost plane, outer part faintly convex anteroventrally. In none of the specimens examined the frill is entirely complete, and the details of its outline are therefore not quite clear. In all specimens where the anterior part of the frill is preserved it decreases considerably in width towards the anterior cardinal corner reaching this corner as a narrow flange (Pl. III, Fig. 9; THORSLUND 1948, Pl. XX, Fig. 9). According to some specimens from Scania belonging probably to this species the frill has posteriorly a more or less similar shape (cf. Pl. III, Fig. 10) except that the width of the frill is considerably smaller than anteriorly. The internal partitions of the frill are relatively wide (Pl. XIV, Fig. 8), as in *Laccochilina*. Subvelar field very low (tr.), concave.

Heteromorphs with an anteroventrally and ventrally convex frill (THORSLUND 1948, Pl. XX, Fig. 9). Anteriorly the dolon extends almost up to the anterior cardinal corner, posteriorly it seems to reach at least to the transverse line tangential to the posterior end of the domicilium, the exact location of the posterior end of the dolon could, however, not be observed on the available specimens.

The lateral surface of the domicilium seems to be ornamented by relatively small tubercles. The details of the ornamentation could not be observed.

The lectotype has the following dimensions: length of the domicilium 1.09 mm; height of the domicilium 0.61 mm; height of the sulcus 0.33 mm. It is, however, apparently considerably smaller than the largest specimens (preserved as internal moulds) examined.

DISCUSSION.—Both dimorphs of this species were described and depicted already by THORSLUND (1948). More numerous, probably conspecific material, preserved mostly as internal moulds, has been collected in the Fågelsång district, Scania, by Dr. M. LINDSTRÖM, and shows an identical dimorphism.

As long as better preserved topotype specimens are not available these internal moulds from Scania are, however, hardly specifically determinable.

The species described was included by HENNINGSMOEN (1953b, p. 49) in *Primitia* (= *Uhakiella*). As the frill of the holotype and also of the material described by HENNINGSMOEN is provided with distinct internal partitions there is, however, no doubt that *A. suecica* represents an eurychilinid. The specimens from 4bγ determined by him as *Primitia suecica* are evidently congeneric with *A. suecica*, but are on the whole too poorly preserved to allow a safe specific determination. They probably belong to a new species.

OCCURRENCE.—*Ludibundus* beds. *Västergötland.*—Kinnekulle, Kullatorp bore (1 tecnom., 1 heterom.). *Scania.*—Fågelsång district (cf. M. LINDSTRÖM 1953), several tecnomorphs and one heteromorph preserved as internal moulds and probably belonging to this species.

Actinochilina sp. A

Pl. III, Figs. 11–12; Text-fig. 17.

DISCUSSION.—A species of *Actinochilina* is fairly common in the *Schroeteri* beds of Västergötland, but the specimens occur in mudstone, and are preserved as specifically indeterminable internal moulds. Only tecnomorphs have been found.

Actinochilina sp. A differs from *A. suecica* by the following characters: (1) in none of the specimens examined does the frill reach the posterior cardinal corner; it narrows conspicuously in posterodorsal direction, and becomes obsolete at about the longitudinal line through the middle of the sulcus; the peripheral edge of the frill appears to be finely denticulate in some small specimens. (2) The ornamentation seems to consist of very small, scattered tubercles, forming an irregular row close to the dorsal margin. There exist certainly also other differences, but owing to the poor state of preservation of the material of both species these differences cannot be defined at present. However, there is not the least doubt that the specimens of *Actinochilina* from the *Schroeteri* beds and those from the *Ludibundus* beds belong to different species.

The specimen figured on Pl. III, Fig. 12 has the following dimensions: length of the lateral surface of the domicilium 1.36 mm; height of the lateral surface of the domicilium 0.72 mm; height of the sulcus 0.38 mm.

Fig. 17. Reconstruction of the probable tecnomorph of *Actinochilina* sp. A after the specimens figured on Pl. III, Figs. 11, 12.

OCCURRENCE.—*Actinochilina* sp. A has been found only in the *Schroeteri* beds of Västergötland. Kinnekulle, Norra Skagen bore (18 tecnom.); Billingen, Stora Åsbotorp bore (8 tecnom.).

Gen. *Platybolbina* HENNINGSMOEN, 1953

1933 *Platychilina*—KUMMEROW (nomen nudum).
1940 *Platychilina*—THORSLUND (non *Platychilina* KOKEN, 1892, nec *Platychilina* KUMMEROW, 1939).
1953a *Platybolbina*—HENNINGSMOEN (nomen nudum).
1953b *Platybolbina*—HENNINGSMOEN (*nom. subst.* pro *Platychilina* THORSLUND, 1940).
non 1939 *Platychilina*—KUMMEROW (non *Platychilina* KOKEN, 1892) = ? *Ectoprimitia* BOUČEK, 1936

TYPE SPECIES.—*Primitia distans* KRAUSE, 1889.

DIAGNOSIS.—Non-sulcate or with a faint, poorly defined sulcal depression. Preadductorial node very faint to absent. Adductorial muscle scar large, well-defined, situated at the mid-height of the domicilium or ventrally of it. Tecnomorphs ventrally and anteroventrally with a plane to concave, fairly broad (tr.) to narrow frill or with a distinct velar ridge. Posterodorsally the frill becomes obsolete in both dimorphs before reaching the posterior cardinal corner, anterodorsally it narrows considerably, reaching the posterior cardinal corner as a narrow flange. Heteromorphs with ventrally and anteroventrally convex frill, forming a dolon.

NOMENCLATORIAL REMARKS.—The nomenclatorial history of the genus *Platybolbina* is rather complicated. Its main facts are as follows:

1933.—KUMMEROW proposed for this genus the generic name *Platychilina*. As neither a definition was given nor any type species designated this name was considered a nomen nudum by ÖPIK (1937, p. 22).

1939.—KUMMEROW (p. 19) defined the genus *Platychilina*, and designated *Primitia elongata* KRAUSE, 1891, as the type species (cf. also RICHTER 1948, p. 178).

1940.—THORSLUND, not being aware of KUMMEROW's paper of 1939, designated *Primitia distans* KRAUSE, 1889, as the type species of *Platychilina*.

1944.—AGNEW (p. 219) pointed out that the ostracode genus *Platychilina* is a junior homonym of *Platychilina* KOKEN, 1892.

1953a.—HENNINGSMOEN (pp. 227–228, 268) proposed the new name *Platybolbina* for *Platychilina* THORSLUND, 1940 (non KOKEN, 1892). As, however, this name was only listed it should be regarded as a nomen nudum.

1953b.—HENNINGSMOEN (p. 50), not being aware of KUMMEROW's paper of 1939, reiterated his proposal of replacing the preoccupied name *Platychilina* THORSLUND by the new name *Platybolbina*. *Primitia distans* KRAUSE, 1889, became the type species of *Platybolbina*.

As *Platychilina* KUMMEROW, 1939, and *Platychilina* THORSLUND, 1940, are based upon different type species, they should be regarded as two different genera, both junior homonyms of *Platychilina* KOKEN, 1892. *Platybolbina* HENNINGSMOEN, 1953b, is the substituted name for *Platychilina* THORSLUND, whereas for *Platychilina* KUMMEROW no substituted name has been proposed so far. The type species of the latter genus is poorly known, frequently obviously misinterpreted, and according to the present writer's opinion certainly not congeneric with *Platybolbina distans* KRAUSE. It may belong to the tvaerenelline genus *Ectoprimita* BOUČEK, 1936, but this cannot be proved at present. Owing to the uncertainty regarding the real characters of the type species of *Platychilina* KUMMEROW, 1939, it is not advisable to substitute a new name for this genus.

SPECIES.—*Primitia distans* KRAUSE, 1889
Primitia plana KRAUSE, 1889
Primitia elongata var. *semicircularis* STEUSLOFF, 1894
Primitia elongata var. *obliqua* STEUSLOFF, 1894
Primitia Kapteyni BONNEMA, 1909
Platybolbina lunulifera HENNINGSMOEN, 1954
Platybolbina temperata SARV, 1956
Platybolbina ampla n. sp.
Platybolbina inflata n. sp.

HENNINGSMOEN (1954b) included also *Primitia elongata* KRAUSE, 1891, *Primitia* (*Ulrichia*?) *umbonata* KRAUSE, 1892, and *Platybolbina tiara* HENNINGSMOEN, 1954, in this genus. The type specimen of *Primitia elongata*, does certainly not belong to *Platybolbina*, but may represent a species of *Ectoprimitia* (cf. above). *Primitia umbonata* and *Platybolbina tiara*, on the other hand, possess an entire, broad frill, resembling that of *Laccochilina* (*Laccochilina*), and in addition also an adductorial pit and a preadductorial node. In the present paper these species are placed in the new genus *Cystomatochilina* (cf. p. 255). The Upper Devonian species *Platychilina praetexta* KUMMEROW, 1939, which was included in *Platybolbina* by HENNINGSMOEN (1954c, p. 54) does not seem to belong to this genus, and it is uncertain whether it is at all an eurychilinid. This species reminds of certain kirkbyids, but the presence of the striated and evidently internally partitioned frill suggests affinities with *Apatobolbina*-like beyrichiids. As long as the presence or absence of the dimorphism is unknown this species can hardly be properly classified.

In addition to the species described in the present paper the South Bothnian erratic boulder Bergsbrunna no. 1 and the *Ludibundus* limestone at Fjäcka, Siljan district, contain a further new species. So far only tecnomorphs have been found which differ from those of the other species described by their relatively very wide frill and by the ornamentation consisting of both a retic-

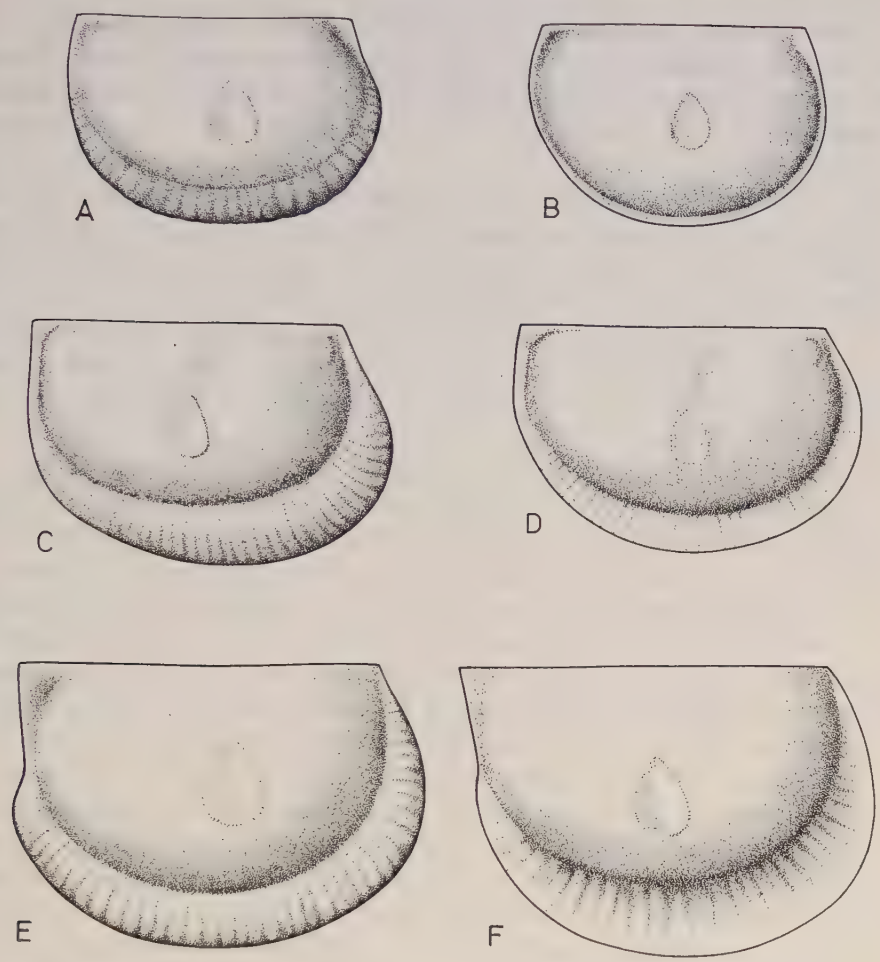


Fig. 18. Reconstructions of *Platybolbina inflata* n.sp. (A–B), *P. kapteyni* (Bonnema) (C–D), and *P. ampla* n.sp. (E–F). To the right heteromorphs (A, C, E), to the left tecnomorphs (B, D, F). Magnification of the heteromorphs ca. × 35. A and E after the holotypes, C after the specimen figured on Pl. IV, Fig. 1. The tecnomorphs have been enlarged so as to equal the heteromorphs in size. B after the specimen figured on Pl. IV, Fig. 6, D after that on Pl. IV, Fig. 3, and F after that on Pl. III, Fig. 15. The reconstruction of the tecnomorph of *P. ampla* (F) of the size corresponding to that of the heteromorph may not be quite correct as the reconstruction was based upon a juvenile specimen.

ulation and coarse tubercles. More material ought, however, to be available before this species can be properly defined.

Generic Characters.—The outline of the lateral surface of the domicilium varies from postplete to nearly amplete. The hinge-line long, as a rule equal to or only slightly narrower than the greatest length of the domicilium. No dorsal ridge. The posterior cardinal corner field is flattened, distinctly defined, and separated from the adjacent part of the domicilium by an abrupt change

in convexity or by a furrow which continues in ventral direction in the furrow between the velum and the domicilium. The anterior cardinal corner field is also flattened but less clearly defined; close to this corner a small node is occasionally present. The dorsum is relatively low, almost plane, and ortho- to epicline.

The adductorial muscle scar is large, ovate, sharply defined, its main part being situated at the mid-length and ventrally of the mid-height of the lateral surface of the domicilium. Dorsally of the muscle scar a faint, poorly defined sulcal depression is developed in some species.

In tecnomorphs the velar structure is of highly variable width: it may be wide (as in *P. ampla*, cf. Pl. III, Fig. 15) or moderately wide (*P. kapteyni*, cf. Pl. IV, Fig. 3) to narrow and ridge-like (*P. temperata*, cf. Sarv 1956 b, Pl. II, Fig. 9–10; *P. inflata*, Pl. IV, Fig. 6).

In all species studied the extension of the frill is remarkably uniform. Posteriorly at about the mid-height of the domicilium it becomes rather suddenly obsolete; dorsally of this point the velar structure is shaped as a rounded velar ridge. Anteriorly the frill decreases considerably in width towards the anterior cardinal corner, and reaches the latter as a narrow flange. In heteromorphs the frill is strongly convex and generally wide. This applies also to species which possess a ridge-like development of the tecnomorphic velar structure (*P. inflata*, Pl. IV, Fig. 5; *P. temperata*, Sarv 1956 b, Pl. II, Fig. 8); the extension of the dolon coincides largely with that of the tecnomorphic frill. In ventral view the contact area between the dolon and the domicilium is situated slightly higher up laterally than that between the corresponding part of the frill and the domicilium in tecnomorphs. There is, however, no such a pronounced upward curve of this contact area in heteromorphs as for instance in *Laccochilina* and *Chilobolbina*, and the ends of the dolon are rather poorly defined. In these respects the dolon of *Platybolbina* seems to be of the somewhat more primitive type than that of *Laccochilina*. The internal structure of the frill is identical with that of other eurychilinids. The internal partitions are fairly coarse (Pl. XIV, Fig. 7). The subvelar field low and concave. No specimen studied showed the actual closure of the valves.

Apart from the ornamentation the best specific characters seem to be furnished by the position and shape of the adductorial muscle scar, the shape of the posterior cardinal angle, and especially by the relative width of the tecnomorphic frill.

Discussion.—By the characters mentioned in the diagnosis *Platybolbina* differs rather clearly from the other eurychilinid genera. It is, perhaps, most similar to *Apatochilina* which is likewise non-sulcate. In *Apatochilina*, however, the frill is entire, extending from one cardinal corner to the other, and the adductorial muscle scar does not seem to be clearly defined. The heteromorphic type is apparently not yet known in this genus, and this fact prevents a closer comparison.

Occurrence.—The earliest species of *Platybolbina* known so far appears in the *Crassicauda* limestone (Upper Llandeilian) of Sweden, and the latest species occurs in the Silurian (*P. lunulifera*). The genus is known from Baltoscandia and from the erratic boulders in Northern Germany and the Netherlands.

Platybolbina kapteyni (Bonnema, 1909)

Pl. IV, Figs. 1–3; Text-fig. 18C–D.

? 1896 *Primitia distans* Krause—Krause, p. 933, Pl. 25, Figs. 7–8.
1909 *Primitia Kapteyni* n.sp.—Bonnema, p. 29, Pl. VI, Fig. 31.
1923b Chilobolbina kapteyni (Bonnema)—Ulrich & Bassler, p. 516.
1934 Chilobolbina kapteyni (Bonnema)—Bassler & Kellett, p. 245.
1937 Eurychilina kapteyni (B.)—Öpik, p. 7.
1940 *Platychilina kapteyni* (Bonn.)—Thorslund, p. 169, Pl. 1, Figs. 8–9, Pl. 5, Fig. 7 [non Pl. 1, Fig. 10 = *Platybolbina* cf. *inflata* n.sp.]
? 1953b *Platybolbina kapteyni* (Bonnema)—Henningsmoen, pp. 50–51, Pl. 1, Fig. 15.
1955 Platybolbina kapteyni (Bonnema)—Sarv, p. 13.
1956a Platybolbina kapteyni (Bonnema)—Sarv, p. 50.

Holotype (by monotypy).—Right tecnomorphic valve, TM no. Os-2309, figured by Bonnema 1909, Pl. IV, Fig. 31.

Type Locality.—Kukruse ("Kuckers"), Estonia.

Type Stratum.—Kohtla zone of the Kukruse Stage ($C_{II}\alpha$).

Diagnosis.—Length of the lateral surface of the domicilium in the heteromorphs 1.05–1.16 mm. Posterior cardinal angle about 90°. Surface of the valve dorsally of the adductorial muscle scar conspicuously depressed. Tecnomorphic velar frill moderately broad, its width (tr.) along the mid-length of the valve about $^1/_6$–$^1/_{10}$ of the height of the lateral surface of the domicilium. Dolon rather wide (tr.), its width along the mid-length of the valve about $^1/_3$–$^1/_4$ of the height of the lateral surface. The lateral surface of the domicilium ornamented by a comparatively coarse and distinct reticulation and small, scattered tubercles.

Description of the Tvären Material.—The preadductorial area of the domicilium less convex than the postadductorial area. Anterodorsally of the muscle scar the surface of the valve is slightly elevated, its summit usually forming the highest part of the valve. Another similar elevation is situated posteroventrally of the muscle scar; the top of this elevation is only slightly lower than that of the elevation in front of the muscle scar. The adductorial muscle scar lies in a faint depression which continues in dorsal direction, extending almost up to the dorsal margin of the valve. The shape and distinctness of this sulcal depression varies within wide limits, but is, nevertheless, invariably present in all specimens studied.

The adductorial muscle scar is well defined, completely smooth, egg-shaped. Its size varies to some extent, but the distance between its ventral end and the frill is in heteromorphs usually equal to, or slightly less, than the length (tr.) of the muscle scar.

The posterior margin of the valve is straight, and meets the dorsal margin under an angle of about 90°. Posterior cardinal corner field flattened, without ornamentation, and separated by a distinct furrow from the adjacent part of the lateral surface. Anterior cardinal corner field also flattened, but not so sharply demarcated from the lateral surface as the posterior corner. Some specimens with a distinct, oblong, smooth node close to the anterior cardinal corner.

Velar frill in tecnomorphs plane or slightly concave, with a distinctly undulate surface, moderately broad, its width along the mid-length of the valve about $^1/_6$–$^1/_{10}$ of the height (tr.) of the lateral surface of the domicilium or even less. The posterior end of the frill is situated somewhat ventrally of the height of the ventral end of the muscle scar. Dorsally of this point the velar structure continues as a rounded velar ridge which in dorsal direction decreases in thickness, and becomes obsolete close to the cardinal corner. Anteriorly the frill reaches the anterior cardinal corner as a narrow flange. Surface of the frill with a fine, concentric striation.

In heteromorphs the dolonal part of the frill is rather strongly convex and considerably broader than the corresponding part of the frill in tecnomorphs. The width (tr.) of the dolon along the mid-length of the valve is about $^1/_3$–$^1/_4$ of the height of the lateral surface of the domicilium along the same line. The posterior end of the dolon coincides with that of the velar frill of the tecnomorphs, its anterodorsal end is less distinct, the shape of the frill changing smoothly from convex to plane before reaching the anterior cardinal corner. This change usually takes place at about the height of the dorsal end of the muscle scar, but may also be situated slightly dorsally or ventrally from this point. In some specimens the frill is slightly convex up to the anterior cardinal corner, and in this case the whole frill is developed as a dolon. The dolon is broadest anteroventrally. In tecnomorphs the contact area between the frill and the domicilium is almost parallel to the free margin of the valve.

On well-preserved valves the lateral surface of the domicilium is ornamented by a distinct, rather coarse reticulation, except for the cardinal corners, the node close to the anterior cardinal corner, and the muscle scar, these latter areas being smooth. On worn valves the reticulation is not distinct, but nevertheless always distinguishable. The well-preserved valves also carry scattered small tubercles, especially on the ventral part of the lateral surface. According to THORSLUND (1940, p. 170) the surface of most valves of this species from Tvären is smooth, but this could not be confirmed on the material studied. A reticulation of varying intensity is developed on all species examined, and also on the valves figured by THORSLUND (1940, Pl. 1, Figs. 8–9) the reticulation is fully visible. No entirely smooth valves of *Platybolbina* were observed by the present writer in the Tvären material.

DIMENSIONS.—See Table 8. All specimens measured have been found in erratic boulders of the Tvären area, Södermanland.

Table 8.

No.	UM Mus. cat. no.	L. domic.	H. domic.	L. valve	H. valve	H-L	Valve	Remarks
1	T 176	1.16	0.66	1.30	0.90	1.12	h—r	Figured on Pl. IV, Fig. 1.
2	T 230	1.08	0.61	1.16	0.80	1.03	h—r	
3	T 140b	1.08	0.63	1.19	0.82	—	h—l	
4	T 177	1.07	0.63	1.16	0.83	—	h—l	Figured on Pl. IV, Fig. 2.
5	T 181	1.07	0.63	1.13	0.79	—	h—l	
6	T 7	1.05	0.63	1.20	0.88	—	h—l	THORSLUND 1940, Pl. 1, Fig. 8.
7	T 184	1.03	0.61	1.09	0.69	0.97	t—l	
8	T 189	1.01	0.57	—	0.63	—	t—r	Figured on Pl. IV, Fig. 3.
9	T 190	0.98	0.56	1.02	0.60	—	t—r	
10	T 188	0.97	0.54	1.03	0.62	0.91	t—l	
11	T 183	0.95	0.56	—	0.64	—	t—l	
12	T 178	0.91	0.52	0.96	0.61	—	t—l	
13	T 192	0.90	0.52	0.93	0.60	—	t—l	
14	T 182	~0.85	0.53	~0.91	0.63	—	t—l	
15	T 140c	~0.80	0.48	~0.83	0.56	—	t—r	
16	T 179	0.78	0.47	0.82	0.54	0.73	t—l	
17	T 185	0.74	0.46	0.80	0.52	0.71	t—r	
18	T 180	~0.74	0.44	0.77	0.48	—	t—l	
19	T 231	0.71	0.43	0.75	0.48	0.66	t—r	
20	T 191	0.70	0.40	0.73	0.47	0.67	t—r	
21	T 186	0.68	0.41	0.71	0.48	—	t—r	
22	T 232	0.68	0.41	0.71	0.47	—	t—l	

DISCUSSION.—*Platybolbina kapteyni* (BONN.) differs clearly from all other species of *Platybolbina* by the combination of the characters mentioned in the diagnosis. As pointed out by THORSLUND (1940, p. 170) the Tvären specimens agree in all essential features with BONNEMA's description and figures.

OCCURRENCE.—*Platybolbina kapteyni* has so far been found with certainty only in the Kohtla zone of the Kukruse Stage of Estonia, in the lowermost *Ludibundus* limestone of the Tvären area, Södermanland, and of the Brunflo-Lockne area, Jämtland (THORSLUND 1940, p. 49). This species was reported by HENNINGSMOEN (1953b) also from 4bγ at Oslo-Asker, but further study is needed in order to ascertain the specific identity of these Norwegian specimens.

Platybolbina ampla n. sp.

Pl. III, Figs. 13–16; Text-fig. 18E–F.

HOLOTYPE.—Right heteromorphic valve, UM no. T 228, figured on Pl. III, Figs. 13–14.

TYPE LOCALITY.—Tvären area, Ringsö, boulders.

TYPE STRATUM.—Lowermost *Ludibundus* limestone.

DERIVATION OF THE NAME.—From Lat. *amplus*, wide.

Diagnosis.—Length of the lateral surface of the domicilium in the heteromorphs 1.29–1.50 mm. Posterior cardinal angle about 80–84°. Lateral surface of the domicilium without any conspicuous depressions. Tecnomorphic velar frill broad, its width (tr.) along the mid-length of the valve about $^1/_3$–$^1/_4$ of the height of the lateral surface of the domicilium. Dolon moderately broad, its width along the mid-length of the valve $^1/_4$–$^1/_6$ of the height of the lateral surface. Lateral surface ornamented by scattered, small, poorly defined tubercles.

Description.—Surface of the valve considerably less convex than that of *P. kapteyni*. Highest convexity immediately posteroventrally of the adductorial muscle scar (Pl. III, Fig. 14). The whole lateral surface of the domicilium is rather uniformly convex, without depressions or elevations similar to those in *P. kapteyni*, except for a very faint elevation in front of the dorsal end of the muscle scar.

Adductorial muscle scar comparatively very large, regularly egg-shaped, completely smooth. The distance between the ventral end of the muscle scar and the frill in heteromorphs slightly less than the length (tr.) of the muscle scar to about $^2/_3$ of the length of the scar; the distance between the dorsal end of the muscle scar and the dorsal margin of the valve about equal to, or slightly shorter than, the height of the muscle scar.

Posterior margin of the valve straight, posterior cardinal angle about 80–84°. Posterior cardinal corner surface flattened, separated from the adjacent part of the lateral surface of the domicilium by a change in convexity only. Anterior cardinal corner field poorly defined.

Extension of the velar frill similar to that in *P. kapteyni*. Tecnomorphic frill undulate, broad, its width (tr.) along the mid-length of the valve about $^1/_3$–$^1/_4$ of the height of the lateral surface of the domicilium. Dolon moderately convex, narrower than in *P. kapteyni*, its width along the transversal mid-line of the valve $^1/_4$–$^1/_6$ of the height of the lateral surface of the domicilium along the same line. Lateral surface of the dolon slightly undulate.

Lateral surface of the domicilium almost smooth, ornamented by small, poorly defined tubercles except for the cardinal corners and the muscle scar which are smooth.

Dimensions.—See Table 9.

Table 9.

No.	UM Mus. cat. no.	L. domic.	H. domic.	L. valve	H. valve	H-L	Valve	Remarks
1	T 227	1.49	0.87	1.60	1.06	1.43	h—r	Holotype. Pl. III, Figs. 13–14.
2	T 228	1.29	0.78	1.43	0.99	1.26	h—r	Figured on Pl. III, Fig. 16.
3	T 229	0.61	0.32	0.65	0.41	0.58	t—l	,, ,, Pl. III, Fig. 15.

Discussion.—The described species differs from *P. kapteyni* by ornamentation, shape of the posterior cardinal angle, delimination of the posterior cardinal corner surface, much narrower dolon, larger adductorial muscle scar, considerably larger size of the heteromorphs, etc. The tuberculate ornamentation of this specimen resembles that of *P. distans* (Krause). The heteromorphic valve of the latter species figured by Krause (1889, Pl. I, Fig. 3a) has, however, a much smaller adductorial muscle scar, a sulcal depression dorsally of the muscle scar, a slightly smaller size (length 1.2 mm according to Krause 1889, p. 16), and evidently a coarser tuberculation. It is still uncertain whether this species of Krause can be identified with certainty on the basis of Krause's description and figure only, since the stratigraphic horizon of the type specimen is unknown.

Occurrence.—Södermanland, Tvären area. Boulders of the lowermost *Ludibundus* limestone (2 heterom., 3 tecnom.).

Platybolbina inflata n. sp.

Pl. IV, Figs. 4–6; Text-fig. 18A–B.

cf. 1940 *Platychilina kapteyni* (Bonn.)—Thorslund, Pl. 1, Fig. 10.

Holotype.—Right heteromorphic valve UM no. T 221, figured on Pl. IV, Figs. 4–5.

Type Locality.—Tvären area, Ringsö, boulders.

Type Stratum.—Lowermost *Ludibundus* limestone.

Diagnosis.—Length of the lateral surface of the domicilium in the heteromorphs 0.96–1.04 mm. Posterior cardinal angle about 90–95°. Lateral surface of the domicilium evenly convex, without depressions. Tecnomorphs with a narrow, ridge-like velar structure, heteromorphs with a strongly convex, inflated dolon. Lateral surface of the domicilium ornamented by distinct, small, closely spaced pits.

Description.—Valves regularly and rather strongly convex, (cf. Pl. IV, Fig. 4), highest convexity in tecnomorphs immediately anterodorsally of the adductorial muscle scar, in heteromorphs usually slightly behind the muscle scar. Lateral surface evenly rounded without depressions. Dorsum very low, almost orthocline.

Adductorial muscle scar well-defined, smooth, ovate. Distance between the ventral end of the scar and the dolon in heteromorphs slightly less than the length (tr.) of the scar, distance between the dorsal end of the scar and the dorsal margin of the valve equal to, or very slightly less than, the length of the scar.

Posterior margin of the valve nearly straight, meeting the dorsal margin at an angle of about 90–95°. Anterior and posterior cardinal corner fields flattened, smooth, separated from the adjacent part of the lateral surface of the domicilium

by a distinct and usually rather broad shallow furrow which continues ventrally into the furrow between the velar structure and the domicilium.

Tecnomorphic velar structure developed as a narrow, distinct, rounded ridge along the whole free margin. Posteriorly the ridge is lower and more rounded than along the other parts of the free edge. Subvelar field concave, low, marginal structures and closure not observed.

Heteromorphs with an inflated, as a rule strongly convex dolon. The convexity of the lateral surface of the dolon usually forms a direct continuation of that of the lateral surface of the domicilium so that in end views the boundary between the dolon and the domicilium appears to be poorly defined externally, especially anteroventrally. It is formed only by a shallow, semisulcus-like furrow. The ventral surface of the dolon is strongly bent down, being hidden in a strictly lateral view. In closed carapace the free margins of the dolon were apparently in contact. In one valve, that figured by THORSLUND (1940, Pl. 1, Fig. 10), the dolon is less convex, the boundary between the dolon and the domicilium well-defined, and the anterodorsal part of the velar structure concave. In the general shape of the domicilium, the ornamentation, and the general size of the adductorial muscle scar this specimen agrees, however, closely with other specimens of *P. inflata*. Until more material is available this specimen is determined as *P.* cf. *inflata*. The dolon of all specimens studied is faintly radially undulate.

Lateral surface of the domicilium ornamented in well-preserved valves by distinct, small, closely spaced pits. In somewhat worn specimens the pits are less distinct, but nevertheless always present at least on the ventral part of the lateral surface of the domicilium.

DIMENSIONS.—See Table 10.

Table 10.

No.	UM Mus. cat. no.	L. domic.	H. domic.	L. valve	H. valve	H-L	Valve	Remarks
1	T 221	1.03	0.64	1.08	0.73	0.96	h—r	Holotype. Pl. IV, Figs. 4–5.
2	T 126	0.97	0.59	1.03	0.73	0.91	h—l	
3	T 225	—	0.66	1.05	0.79	—	t—l	
4	T 222	—	—	0.85	0.55	—	t—r	
5	T 223	—	—	0.82	0.54	0.68	t—r	Figured on Pl. IV, Fig. 6.
6	T 224	—	0.48	0.78	0.51	0.70	t—l	

DISCUSSION.—*Platybolbina inflata* differs distinctly from all other species of *Platybolbina* especially by its narrow, ridge-like tecnomorphic velar structure, ornamentation, and the inflated, strongly convex dolon. By its reduced tecnomorphic velar structure this species reminds to certain extent of *Oepikella*, and is in fact the most *Oepikella*-like chilobolbine species known.

poorly defined anteriorly, where it is marked only by a faint change in convexity. Posteriorly the dolon reaches to about the mid-length of the post-adductorial area. Farther in posterodorsal direction the velar structure is developed as a rounded ridge, and higher dorsally, close to the cardinal corner, as an indistinct bend. The anterodorsal end of the dolon reaches almost up to the anterior cardinal corner. The inner, plane part of the dolon shows a faint undulation.

The lateral surface of the domicilium is covered by minute closely spaced granules (too minute to be visible in the photographs at the magnification of × 25) and relatively large tubercles of somewhat varying size. The proximal, plane part of the dolon has the same ornamentation, except that the tubercles are only few in number. The minute granules are for the most part arranged in rows so as to give the ornamentation sometimes a very finely reticulate appearance.

Dimensions of the holotype.—Length of the valve 1.34 mm; height of the valve 0.95 mm; length of the lateral surface of the domicilium 1.20 mm; height of the lateral surface of the domicilium 0.73 mm.

Discussion.—As long as the development of the tecnomorphic velar structure is unknown the generic reference of this species is somewhat uncertain. As, however, the heteromorphs exhibit a close similarity to those of *P. geniculata* the species described belongs in all probability to *Piretia*.

The specimens figured by Krause (1891, Pl. XXXI, Figs. 6, 7) as *Primitia* aff. *Jonesii* Krause resemble the species described. The heteromorphic valve figured by him has also approximatively the same size (length 1.43 mm according to Krause 1891, p. 494) as that of *P. clypeolaria*. The sulcus is, however, slightly shorter in Krause's figures, and the details of the ornamentation cannot be compared, the figures of Krause being too schematical in this respect. The general appearance of the ornamentation is, however, closely similar. According to Krause the specimens figured by him were found in a grey "*Beyrichia*" limestone, and thus probably come from a higher stratigraphic horizon (*Schroeteri* limestone?) than *P. clypeolaria*. They may be conspecific with the latter species, but this cannot be proved at present.

Occurrence.—*Piretia clypeolaria* has been found so far only in the *Platyurus* limestone.

Öland.—Skärlöv bore (1 heterom.). *Östergötland*.—Motala bore (2 tecnom.).

Gen. *Uhakiella* Öpik, 1937

Type Species.—*Uhakiella coelodesma* Öpik, 1937.

Diagnosis.—Unisulcate, with a distinct adductorial pit. Some species with a flattened, indistinct ventral lobe, a ridge around the ventral part of the sulcus, and close to each cardinal corner with a low, rounded dorsal plica; other species without any conspicuous elevations on the lateral surface of the

domicilium. Tecnomorphs with a frill-like velar flange, velar ridge, or without a velar structure. Heteromorphs with a strongly convex velar dolon; the inner part of the lateral surface of the dolon lies almost at the same level as the general lateral surface of the domicilium, and has usually also the same type of ornamentation.

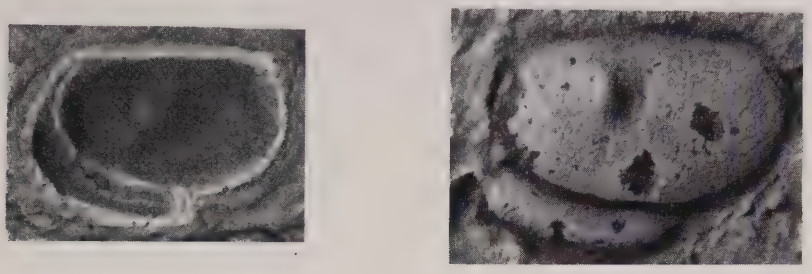
SPECIES.—*Beyrichia strangulata* SALTER, 1851.[1]
Beyrichia granulifera ULRICH & BASSLER, 1909
Uhakiella coelodesma ÖPIK, 1937
Uhakiella kohtlensis ÖPIK, 1937
Uhakiella pumila ÖPIK, 1937
Bromidella linnarssoni HENNINGSMOEN, 1948
Primitia osloensis HENNINGSMOEN, 1954
Uhakiella aequigranosa n. sp.
Uhakiella periacantha n. sp.

HENNINGSMOEN (1953b) included also *Eurychilina* [= *Actinochilina*] *suecica* THORSLUND, 1948, in *Primitia* (= *Uhakiella*) but this species is certainly an eurychilinid (cf. p. 258).

GENERIC CHARACTERS.—The outline of the species of *Uhakiella* varies from nearly amplete to rather strongly postplete. The adductorial pit is as a rule rather deep in its deepest part, its outline varies from rounded to oblong or quadrangular. The dorsum is low to moderately high, usually slightly epicline.

In several species the lateral surface of the domicilium shows a characteristic arrangement of lobes and ornamental ridges. Their general pattern has been represented diagrammatically by ÖPIK (1937, p. 43, Fig. 5). The ventral end of the adductorial pit is surrounded by a rounded horseshoe-shaped ridge, the anterodorsal end of which is expanded, and forms a more or less distinct preadductorial node ("node-like middle lobe" in ÖPIK loc. cit.). Posterodorsally the ridge merges into an indistinctly delimited, rather large elevation (= anterior lobe in ÖPIK, loc. cit.) which is, however, scarcely visible in most species. The horseshoe-like swelling is delimited ventrally by a faint depression, and ventrally of it the surface of the valve is inflated forming a flattened ventral

[1] It is difficult to ascertain the exact date of erection of this species. The species was described as "n. sp." by SALTER (1854, p. II, Pl. 1E, Figs. 1, 1a, 1b) in the Appendix A to "A Synopsis of the Classification of the British Palaeozoic Rocks" by SEDGWICK. The introduction of the Appendix is dated by SALTER Febr. 1852 indicating possibly the date when his manuscript was finished. On p. 136 of the "Synopsis" the species was redescribed by MCCOY who referred for the illustration to the plate in SALTER's Appendix. According to HILL (1938, p. 45) the page 136 of the "Synopsis" was published in 1851. If her dating is correct the redescription of the species by MCCOY appeared before the termination of SALTER's manuscript. MCCOY, however, clearly states that SALTER is the author of the species, and he also undoubtedly had access to SALTER's manuscript. Therefore, SALTER must be regarded as the author of the species, and if the description by MCCOY appeared in 1851, this date should be taken as the date of this species. The present writer is indebted to Dr. O. M. B. BULMAN for the information concerning the dating of different parts of the "Synopsis".



A B

Fig. 23. A, internal view of a right heteromorphic valve of *Uhakiella* cf. *coelodesma* Öpik. UM no. Vg. 88. Västergötland, Kinnekulle, Kullatorp core, 86.47 m. × 15. B, internal mould of a left heteromorphic valve of *Uhakiella strangulata* (Salter, 1851). SMC no. 29986. Coniston, Lancashire, probably Coniston limestone. Presumably one of the specimens figured by Salter 1854, Pl. 1 E as *Beyrichia strangulata*. × 20.

lobe. Close to the anterior cardinal corner a more or less distinct ridge is developed (= posterior lobe in Öpik loc. cit.) which evidently corresponds to the anterior part of the dorsal plica in some other piretellids. Near the posterior cardinal corner the posterior part of the dorsal plica is occasionally present. Both arches of the dorsal plica are not connected in any species of *Uhakiella* hitherto described. The relief of the lateral surface of the domicilium of the type described above is most clearly expressed in *Uhakiella coelodesma*, *U. granulifera*, and *U. kohtlensis*, and very feebly developed, but discernible in *U. aequigranosa* and *U. periacantha*. In the other species of *Uhakiella* only the preadductorial node seems to be present.

Tecnomorphs of *U. strangulata* and *U. coelodesma* have a velar ridge, those of *U. kohtlensis* and *U. linnarssoni* a moderately wide velar flange which is frill-like in *U. kohtlensis*. *Uhakiella periacantha* does not seem to possess any tecnomorphic velar structure. In heteromorphs the dolon is always strongly convex, the contact area between the dolon and the domicilium placed high upon the side of the valve, lying anteroventrally at about the same general level as the lateral surface of the domicilium. The external boundary between the lateral surface of the dolon and that of the domicilium is as a rule fairly indistinct, in part owing to the usually identical ornamentation on both surfaces. No closed heteromorphic carapaces of *Uhakiella* have been found so far, but as the peripheral surface of the dolon is broad (tr.) and almost vertically directed the free edges of the dolon were apparently in contact in closed carapaces. The subvelar field of both valves possesses a ridge, but the exact position of these ridges as well as the closure of the carapace along the free edge are still incompletely known.

Discussion.—*Uhakiella* was by E. A. Schmidt (1941, p. 33) regarded as a junior subjective synonym of *Bromidella*. Henningsmoen (1948) and Thorslund (1948) joined this opinion. Later Henningsmoen (1953a, p. 226) considered "the strong dorsal ridge or rather swelling of *Bromidella* to be rather

unique", and concluded that it might be better to retain *Bromidella* as a separate genus. An examination of several specimens of the type species of *Bromidella* by the present writer has shown this genus to differ distinctly from *Uhakiella*. In *Bromidella reticulata* HARRIS (cf. Pl. IV, Fig. 23) the dorsum is fairly high (tr.) and strongly epicline. The dorsal plica is prominent, continuous along the whole dorsal margin, and its posterior part is thickened into a ventrally indistinctly delimited, mainly ornamental elevation. The preadductorial node is high and prominent. Also other species of *Bromidella* described by KAY (1940) possess these characters.

HENNINGSMOEN (1953a, b; 1954b) treated *Uhakiella* as very close to, or possibly identical with, *Primitia*. His definition of the latter genus was based on a re-examination of the type material of *Beyrichia strangulata* which species was designated as the type species of *Primitia* by MILLER (1889; cf. WARTHIN 1948, p. 645). As, however, an application will be submitted to the International Commission on Zoological Nomenclature for preserving the accustomed usage of the generic name *Primitia* (cf. p. 217) with *Primitia mundula* as the type species, this generic name will be transferred to a group of species of *Leperditellacea*. The type material of *Beyrichia strangulata* has been re-examined also by the present writer, and according to his observations there remains scarcely any doubt of this species belonging to a group of *Uhakiella* characterized by a narrow tecnomorphic velar ridge and by the absence of ornamental ridges or conspicuous elevations on the lateral surface of the domicilium. The type material of *U. strangulata* consists of internal moulds and external imprints, and the state of preservation is not especially favourable. Some of the specific characters are, therefore, incompletely known. The heteromorphs (Fig. 23B; cf. also the diagrammatic reconstruction by HENNINGSMOEN 1953a, p. 225, Fig. 11b) possess a strongly convex dolon. The ornamentation consists of fairly large scattered tubercles. The length of the heteromorphic valves slightly exceeds 2 mm. Without examination of a better preserved material of *U. strangulata*, it will, however, be difficult to distinguish this species from other species of the same group of *Uhakiella* with about the same type of ornamentation.

OCCURRENCE.—The earliest species of *Uhakiella* known so far appears in the Lasnamäe Stage (Lower Llandeilo) of Estonia (cf. SARV 1956a). No Silurian species referable to this genus are known. Hitherto the genus is unknown outside Europe.

Uhakiella cf. *coelodesma* ÖPIK, 1937

Pl. V, Figs. 6–9; Text-fig. 23A.

cf. 1937 *Uhakiella coelodesma* n.sp.—ÖPIK, pp. 43–44, Pl. III, Figs. 1–3.
1940 *Uhakiella coelodesma* ÖPIK—THORSLUND, p. 172, Pl. I, Figs. 6, 7.
1948 Bromidella coelodesma (ÖPIK)—THORSLUND, pp. 350, 359.

DESCRIPTION.—The following description of the tecnomorphs is based upon the specimens from the Tvären area, and that of the heteromorphs upon speci-

mens from the Kullatorp core. In the boulders of the Tvären area no heteromorphs have been found so far, and in the bores of Västergötland all tecnomorphs are poorly preserved.

Adductorial pit relatively large, somewhat quadrangular in outline, surrounded ventrally and anteriorly by a distinct rounded ridge, which culminates anterodorsally in a low node and posteriorly in a poorly defined inflation. Dorsally of the adductorial pit the surface of the valve is faintly depressed. A broad, shallow depression is developed ventrally of the horseshoe-shaped ridge. Ventrally from this depression the ventral part of the lateral surface of the domicilium is faintly inflated forming a flattened ventral lobe. A rather distinct anterior arch of the dorsal plica is situated close to the anterior cardinal corner, and on some specimens from the Tvären area a corresponding plica is developed also posteriorly. The posterior arch of the dorsal plica is always lower and less distinct than the anterior arch. The peripheral part of the lateral surface of the domicilium is usually rather distinctly flattened ventrally of the ventral lobe in tecnomorphs.

Tecnomorphs with a narrow, rounded, bend-like velar ridge. Right valve with an admarginal ridge fairly close to the velar ridge, the left valve with a marginal ridge close to the free edge. The ridges on the subvelar field of both valves have a row of spines (cf. THORSLUND 1940, Pl. 1, Figs. 6, 7) which, however, are often broken off. The ridges then appear to bear a row of tubercles (cf. Pl. V, Fig. 8). The actual closure of the carapace was not observed, but evidently the left valve overlaps the right one along the free edge.

Dolon strongly convex, rather broad, anterior end reaching up to about the longitudinal line through the middle of the adductorial pit, posterior end to about the anterior third of the postadductorial area. Externally there is no distinct boundary between the dolon and the lateral surface of the domicilium.

The ornamentation consists of closely spaced tubercles, relatively large on the inflations and small in the depressions. The tubercles continue also upon the inner part of the lateral surface of the dolon. In all examined specimens from the Tvären area and from Östergötland the tubercles are lower and more indistinct than in those from Västergötland.

DIMENSIONS.—See Table 13.

DISCUSSION.—The specimens described are very similar to *Uhakiella coelodesma* ÖPIK, and no definite differences can be pointed out. There may, however, exist differences in the ornamentation as this cannot be observed clearly enough on ÖPIK's (1937, Pl. III, Figs. 1–3) figures, and since no Estonian material has been at the author's disposal for comparison, it is safer at the time being not to attempt a definite identification. The Swedish material also occurs in a slightly higher stratigraphical horizon than the Estonian. The differences, if present, are, however, probably of merely subspecific value. On the other hand, the possibility must be taken into account that the differences in ornamentation between the specimens from Västergötland and those from

Table 13.

No.	Mus. cat. no.	L. valve	H. valve	L. domic.	H-L	Valve	Locality	Remarks
1	UM Vg. 87	2.55	1.69	2.40	—	h—l	Kullatorp 86.47 m	Figured on Pl. V, Fig. 6.
2	UM Vg. 88	2.37	1.59	—	1.53	h—r	,, ,, ,,	
3	UM T 5	1.78	1.11	—	1.31	t—r	Tvären, Ringsö	Thorslund 1940, Pl. 1, Fig. 6.
4	UM T 6	1.76	1.11	—	1.33	t—l	,, ,,	Thorslund 1940, Pl. 1, Fig. 7.
5	UM T 95	1.51	0.95	—	1.13	t—r	,, ,,	Figured on Pl. V, Figs. 7–8.
6	SGU	1.22	0.79	—	—	t—r	Smedsby Gård 96.37 m	Figured on Pl. V, Fig. 9.

the other districts might indicate the presence of two different species or subspecies also in Sweden.

The specimen of *Bollia granulosa* Krause figured by Krause (1889) on Pl. II, Fig. 1 was referred by Öpik (1937, p. 43) to *U. coelodesma*. The figure by Krause shows, however, a rather different ornamentation, and the reference is, therefore, highly uncertain. Also *Primitia* aff. *Jonesi* Krause, figured by Krause 1891, Pl. XXXI, Fig. 6 was referred by Öpik (loc. cit.) to this species. But, as pointed out by Thorslund (1940, p. 172) this is not a likely assumption. In the present writer's opinion this specimen figured by Krause probably belongs to *Piretia* (cf. p. 285).

Occurrence.—*Uhakiella* cf. *coelodesma* has been found in Sweden only in the lower part of the *Ludibundus* beds. In Estonia *U. coelodesma* occurs according to Sarv (1956a, p. 53) in the Lasnamäe Stage (C_1b) and in the lower part of the Uhaku Stage (C_1c). Its occurrence in C_1b needs, however, further confirmation.

Södermanland, Tvären area, erratic boulders (3 tecnom.). *Öland*.—Böda Hamn bore (2 tecnom.). *Östergötland*.—Smedsby Gård bore (2 heterom., 2 tecnom.). *Västergötland*, Kinnekulle.—Kullatorp bore (2 heterom., 1 tecnom.); Norra Skagen bore (2 heterom., 1 tecnom.).

Uhakiella aequigranosa n. sp.

Pl. V, Figs. 10–11.

Holotype.—Left heteromorphic valve, UM no. D 427, figured on Pl. V, Fig. 10.

Type Locality.—Fjäcka, locality no. 4 (cf. Jaanusson 1947, p. 44, Fig. 2).

Type Stratum.—Uppermost *Crassicauda* limestone.

Derivation of the Name.—The name refers to the ornamentation which consists of tubercles of about uniform size.

DIAGNOSIS.—Length of the heteromorphs about 2,1 mm. Ornamental ridges very faint, scarcely discernible. No distinct external boundary between dolon and domicilium. In posterior direction the dolon reaches to about the mid-length of the postadductorial area. Surface ornamented with relatively large, closely spaced tubercles of about uniform size all over the lateral surface of the domicilium and the inner part of the lateral surface of the dolon.

DESCRIPTION.—Outline almost amplete to slightly preplete. Lateral surface of the domicilium rather faintly convex, highest convexity somewhat behind the adductorial pit. Adductorial pit oblong, of moderate size, surrounded, except dorsally, by a poorly defined, scarcely discernible, horseshoe-shaped ridge, the anterodorsal end of which terminates in an indistinct, flattened preadductorial node. A very indistinct and faint trace of a dorsal plica can be observed near the anterior cardinal corner.

In tecnomorphs the details of the peripheral part of the valve have not been accessible to clear observation, it proving very difficult to clean the specimens from a hard matrix. No velar structure seems, however, to exist or perhaps only a very faint velar ridge.

In the heteromorphs the dolon is anteroventrally strongly convex, pouch-like. The anterodorsal end of the dolon reaches to about the longitudinal line through the middle of the preadductorial pit or slightly farther in dorsal direction. The posterior end reaches to about the mid-length of the post-adductorial area. Externally no distinct boundary is present between the lateral surface of the domicilium and the inner part of the dolon.

The ornamentation consists of relatively large, closely spaced tubercles of about uniform size all over the lateral surface of the valve and the inner part of the dolon. The diameter of the tubercles much exceeds the distance between the tubercles.

DIMENSIONS.

	Left heteromorphic valve. Holotype	Right tecnomorphic valve. Figured on Pl. V, Fig. 11
Length of the valve	2.10	1.27
Height of the valve	1.46	0.82

DISCUSSION.—By its ornamentation and the indistinct ornamental ridges *U. aequigranosa* differs clearly from other species of *Uhakiella* from Balto-scandia. The arrangement of the ridges is on the whole identical with that in *U. coelodesma*, but the ridges are very faint. The ornamentation of *U. aequigranosa* resembles to a certain extent that of *U. strangulata*. In the latter species, however, the tubercles are not so closely spaced as in *U. aequigranosa*, the distance between the tubercles being usually twice the diameter of tubercles or greater.

Occurrence.—*Uhakiella aequigranosa* n.sp. has only been found in the *Crassicauda* limestone of Sweden.

Siljan district, Dalarna.—Fjäcka (1 heterom., 1 tecnom.). *Öland*.—Gammalsby bore (1 heterom., 3 tecnom.). *Östergötland*.—Motala bore (2 tecnom.).

Uhakiella periacantha n. sp.

Pl. V, Figs. 12–17; Text-figs. 6, 24, 25.

Holotype.—Left heteromorphic valve, UM no. B 211, figured on Pl. V, Figs. 13–14.

Type Region.—South Bothnian area. The holotype was found in the erratic boulder Bergsbrunna no. 1.

Type Stratum.—Uppermost beds of the *Crassicauda* limestone.

Derivation of the Name.—The name refers to the marginal spines along the entire free margin.

Diagnosis.—Length of the heteromorphs (excluding the marginal spines) 1.15–1.30 mm. Nodes and ridges very faintly developed. Tecnomorphs with-

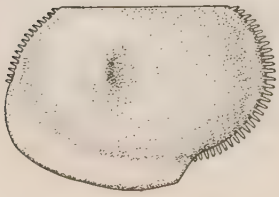


Fig. 24. Reconstruction of a heteromorphic valve of *Uhakiella periacantha* n.sp. Number and size of the marginal spines are approximative. × 40.

Fig. 25. *Uhakiella periacantha* n.sp. Diagrammatic drawing of a transversal section of a heteromorph. After a thin section, cf. Pl. XIV, Fig. 2. × 50.

out velar structure. Boundary between lateral surface of the dolon and that of the domicilium marked by a shallow furrow. The posterior end of the dolon reaches to about the mid-length of the postadductorial area. Marginal spines along whole length of the free edge. The ornamentation consists of minute, closely spaced tubercles. Their diameter is usually about equal to the distance between the tubercles. Dolon with faint radial striation.

Material.—11 heteromorphic, 20 tecnomorphic valves.

Description.—Domicilial outline slightly postplete or nearly amplete; highest convexity somewhat behind the adductorial pit. Dorsum low, slightly epicline. Adductorial pit of varying size, sometimes rather small (Pl. V, Fig. 13), occasionally also moderately large (Pl. V, Fig. 15), oblong. The pit is sur-

Table 14.

No.	UM Mus. cat. no.	L. valve	H. valve	L. domic.	H. domic.	H-L	Valve	Remarks
1	B 223	1.28	0.91	1.19	0.75	—	h—l	
2	B 216	1.24	0.88	1.16	—	0.76	h—l	
3	B 229	1.24	0.82	1.16	0.68	0.68	h—l	
4	B 228	—	0.84	—	0.68	—	h—r	
5	B 211	1.24	0.86	1.15	0.69	0.76	h—l	Holotype. Pl. V, Figs. 13–14.
6	B 212	1.24	0.87	1.15	0.71	—	h—l	Figured on Pl. V, Fig. 15.
7	B 213	1.20	0.83	1.13	0.69	0.72	h—r	,, ,, Pl. V, Figs. 16–17.
8	B 230	1.16	0.79	1.11	0.66	0.76	h—r	
9	B 220	1.04	0.69	—	—	—	t—l	
10	B 226	1.03	0.70	—	—	0.70	t—l	Figured on Pl. V, Fig. 12.
11	B 219	1.03	0.69	—	—	—	t—l	
12	B 218	1.00	0.67	—	—	—	t—l	
13	B 227	0.88	0.57	—	—	0.61	t—l	
14	B 222	0.88	0.57	—	—	0.64	t—l	
15	B 224	0.87	0.56	—	—	0.61	t—r	
16	B 285	0.86	0.55	—	—	—	t—r	
17	B 215	0.82	0.56	—	—	0.60	t—l	
18	B 217	0.77	0.51	—	—	0.58	t—l	
19	B 214	0.74	0.50	—	—	—	t—l	
20	B 221	0.72	0.48	—	—	0.53	t—r	
21	B 225	0.70	0.47	—	—	—	t—r	

rounded, except dorsally, by a low and indistinct horseshoe-shaped ridge with the anterodorsal end culminating in a low poorly defined node. Anteroventrally of the horseshoe-shaped ridge the surface of the domicilium is faintly depressed. A faint trace of a dorsal plica near the anterior cardinal corner, no such trace posteriorly.

In tecnomorphs no trace of a velar structure has been observed. Dolon strongly convex, peripheral part steeply sloping. The anterior end of the dolon reaches to about the longitudinal line through the middle of the preadductorial pit, the posterior end to about the mid-length of the postadductorial area. The boundary between the dolon and the domicilium is marked externally by a shallow, indistinct furrow, or, rather, a faint change in convexity.

A row of marginal spines is developed along the whole free margin. The width of each spine is about equal to the distance between the spines, and the length of each spine seems usually to be about twice the width. The spines were, however, as a rule rather badly preserved, and the above data about their proportions are only approximative.

The ornamentation of the lateral surface of the domicilium consists of minute, closely spaced tubercles, the diameter of the tubercles being roughly equal to the distance between the tubercles. The tubercles continue also on

the proximal part of the dolon, but are smaller there. The dolon carries, furthermore, a faint radial striation.

Dimensions.—See Table 14. In measuring the length and the height of the valve the marginal spines have been excluded.

Discussion.—By its small size and by its ornamentation *U. periacantha* differs distinctly from the other species of *Uhakiella* described so far. The most closely similar species seems to be *U. pumila* Öpik which according to Öpik's figure (1937, Pl. III, Fig. 5) has also a similar row of marginal spines. In *U. pumila*, however, according to the figure of the holotype in Öpik (1937) the adductorial pit has a slightly more dorsal position, and is rather indistinctly delimited dorsally, thus resembling a short sulcus. Moreover, the dolon is considerably shorter.

Occurrence.—*Uhakiella periacantha* n.sp. has been found only in the South Bothnian erratic boulder Bergsbrunna no. 1 in which it is a rather common species.

Subfam. TVAERENELLINAE nov.

Diagnosis.—Dolon faintly to moderately convex, its peripheral edges not in contact in closed carapaces, but separated by a broad or moderately broad space.

Genera.—*Dicranella* Ulrich, 1894
? *Ectoprimitia* Bouček, 1936
Hesperidella Öpik, 1937
Euprimites Hessland, 1949
Tvaerenella n.gen.
Levisulculus n.gen.

Discussion.—This subfamily consists of two rather distinct groups of genera, one of them including *Hesperidella* and *Dicranella*, and the other the remaining genera. There is scarcely any doubt that the genera within each group are closely related. The main difference between the groups lies in the shape of the preadductorial node which is developed as a knob or spine in the *Hesperidella* group, but as a flattened and often indistinct node in the *Tvaerenella* group. The possibility of expressing the difference between these groups also in the classification has been considered. No step in this direction has, however, been found advisable for the time being, mainly on account of difficulties in formulating sufficiently sharp diagnoses. The shape of the dolon is very similar in both groups, but may have originated independently along two different lines. In order to answer this question more species of both groups will have to be studied. The *Hesperidella* group resembles the *Piretellinae* more than does the *Tvaerenella* group, and is apparently more closely related to it. *Parabolbina*

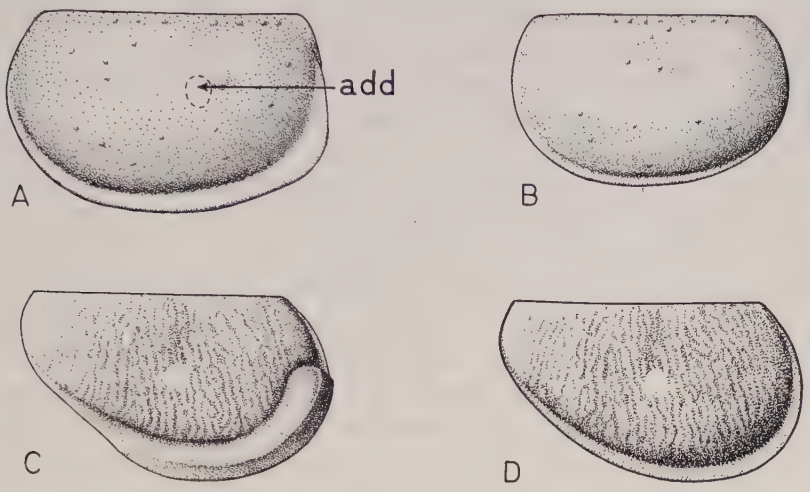


Fig. 26. Reconstructions of (A, B) *Tvaerenella carinata* (THORSL.) and (C, D) *Levisulculus lineatus* n.sp. × 35. *add* = the position of the scar of the adductor muscle. To the left heteromorphs (A, C), to the right tecnomorphs (B, D).

staufferi KAY, 1940, (if erected on heteromorphs) and *Parabolbina carinifera* KAY, 1940, (if erected on tecnomorphs) seem to belong to the *Hesperidella* group of *Tvaerenellinae*. As pointed out also by HENNINGSMOEN (1953a, p. 239) they have certainly nothing in common with *Parabolbina*. If the interpretation of their probable dimorphism as given above is correct, a new genus must be erected for their inclusion. Representatives of one or two further new genera of the *Tvaerenella* group have been examined by the present writer, but their description lies outside the scope of the present paper.

The type species of *Ectoprimitia* BOUČEK, 1936, may be a member of the *Tvaerenellinae* of the *Tvaerenella* group. As, however, the type species, *Primitia corrugata* KRAUSE, 1892, is poorly known (the specimen figured by KRAUSE 1892 being the only one found by him and, moreover, apparently lost) the genus can hardly be characterized at present. HESSLAND (1949, pp. 224–225) considered *Ectoprimitia* to be similar to *Primitiella* from which it differs, in his opinion, by a deeper, narrower, and more dorsally extending sulcus. According to his interpretation the flange along the free margin in *Primitia corrugata* KRAUSE, 1892, is a depressed marginal zone, and not a velar structure. It is, however, difficult to see why HESSLAND considered the "Saum" (KRAUSE 1892, p. 386) in this species to be a marginal structure, the present writer is inclined to regard it as a narrow velar flange similar to that in tecnomorphs of *Levisulculus*. According to the latter interpretation *Ectoprimitia tenuireticulata* HESSLAND, 1949, is not an *Ectoprimitia*, but belongs somewhere in the proximity of *Primitiella*. *Ectoprimitia corrugata krausei* BOUČEK, 1936, occurs in much younger strata (Ludlow, eβ, cf. BOUČEK 1936, p. 45) than the type species, and

as long as it is not known whether or not it possessed a velar dimorphism, the generic reference is highly uncertain.

Occurrence.—The earliest *Tvaerenellinae* known so far appear in the "*Raniceps*" limestone of Baltoscandia (*Euprimites*, *Tvaerenella*).

Gen. *Tvaerenella* n. gen.

Type Species.—*Primitiella carinata* Thorslund, 1940.

Derivation of the Name.—After the Tvären area in which the type species is occasionally rather common.

Diagnosis.—No sulcus or merely a faint sulcal depression. A moderately large large muscle scar is situated somewhat dorsally of the mid-height of the lateral surface of the domicilium. Tecnomorphs with a more or less distinct velar ridge; heteromorphs with a usually rather long, slightly convex, flange-like dolon, broadest anteroventrally.

Species.—*Primitiella*? *carinata* Thorslund, 1940
Primitiella granosa Öpik, 1937
? *Primitiella pulex* Öpik, 1937
Apatochilina ubjaensis Öpik, 1937
? *Primitiella magna* Sarv, 1956
? *Primitiella longa* Sarv, 1956.

According to Sarv (1956a, p. 51) *Primitiella indistincta* Öpik, 1937, is conspecific with *P. granosa*. *Apatochilina ubjaensis* is based most probably on heteromorphs of a species of *Tvaerenella* (cf. p. 299). *Primitiella pulex* Öpik has an outline rather different from the other species referred here to *Tvaerenella* reminding in this respect of *Levisulculus*, and as long as the heteromorphs and the location of the muscle scar are unknown, this species can only tentatively be referred to *Tvaerenella* (cf. also p. 322). The published figures of "*Primitiella*" *magna* and "*P.*" *longa* are too poor for a safe generic reference of these species.

Generic Characters.—The genus *Tvaerenella* can be best characterized as an *Euprimites* without sulcus or with merely a faint sulcal depression. In other characters this genus is very similar to *Euprimites*. "*Euprimitia*" *plena* Öpik seems to occupy a somewhat intermediate position between *Tvaerenella* and *Euprimites*, but by its rather narrow, though shallow, sulcus stands apparently closer to the latter genus.

Within the genus *Tvaerenella* as defined in the present paper, forms without any trace of a sulcus, like *T. pulex*, as well as species with a rather distinct, but poorly defined sulcal depression are united. Both these types seem to be joined by a morphological series which in this respect is rather continuous. In front of the sulcal depression a small, low presulcate node can be developed, and posteroventrally of the node a rounded, smooth muscle scar can usually

be distinguished. The latter is situated dorsally of the mid-height of the domicilium (Fig. 26 A) and thus has a position closer to the dorsal margin than that of *Levisulculus*. The dorsum is rather low, almost orthocline to slightly epicline.

Tecnomorphs with a velar ridge, resembling that of *Euprimites*. This ridge may, however, be weak and bend-like even in rather late instars. The dolon in heteromorphs is moderately broad, slightly convex, and flange-like, resembling that of *Euprimites*. The contact area between the dolon and the domicilium is placed rather considerably higher upon the side of the domicilium than that between the corresponding part of the velar structure and the domicilium in the tecnomorphs. At present the dimorphism is known only in the type species.

Upon the subvelar field both valves carry a strong ridge. As in *Euprimites* the marginal ridge of the left valve is as a rule slightly stronger than that of the right valve (cf. Pl. VI, Fig. 4; Öpik 1937, Pl. XIII, Fig. 9). The left valve seems to overlap the right valve to some extent along the free margin, but the details of the overlap have so far not been accessible to investigation.

Discussion.—Formerly the species included here in *Tvaerenella* have generally been placed in *Primitiella*. The latter genus is, however, non-velate, and belongs to quite a different group of palaeocope ostracodes.

Occurrence.—The earliest species of *Tvaerenella* known to the present writer occurs in the "*Raniceps*" beds of Western Estonia. In a piece of Pakri calcareous sandstone from the Island of Väike Pakri (Lilla Rågö) collected by G. Holm (RM no. Ar. 30002) the present writer has found a heteromorphic valve which evidently belongs to *Tvaerenella*. The other species known at present come from the Middle Ordovician and the lowermost Upper Ordovician. Outside Baltoscandia the genus is unknown.

Tvaerenella carinata (Thorslund, 1940)

Pl. VI, Figs. 4–9; Text-fig. 26A–B.

1940 *Primitiella ? carinata* n.sp.—Thorslund, p. 163, Pl. 4, Fig. 8.

Holotype.—Left heteromorphic valve figured by Thorslund 1940, Pl. 4, Fig. 8 (SGU).

Type Locality.—Exposure 1.2 km W of the Tandsbyn railway station, Brunflo-Lockne area, Jämtland.

Type Stratum.—Lower *Ludibundus* limestone.

Diagnosis.—Length of heteromorphs 1.10–1.20 mm. Outline nearly amplete. Domicilium with an indistinct sulcal depression and with a small, flattened preadductorial node in front of it. Ornamentation consisting of a faint reticulation and scattered, rather small tubercles.

Material.—5 heteromorphic and 15 tecnomorphic valves and carapaces.

Description.—Outline nearly amplete or faintly postplete, domicilium rather strongly and more or less regularly convex. The highest convexity lies

slightly behind the sulcal depression, somewhat ventrally of the middle of the valve. The length and convexity of the valves vary rather considerably as also observed by Öpik (1937, p. 14) in *T. granosa*. Dorsum moderately high, almost orthocline, its lateral margin formed usually by a sharp edge which in some specimens is slightly raised and ridge-like. The surface ventrally of the edge usually carries an irregular row of tubercles.

In front of the mid-length of the domicilium the surface is slightly depressed, forming a faint, poorly defined sulcal depression. In front of the depression the surface is slightly elevated forming a low, flattened preadductorial node which is scarcely discernible in some specimens. The area posteroventrally of the preadductorial node carries a rounded, moderately large adductorial muscle scar, situated slightly dorsally of the mid-length of the domicilium (Fig. 26 A). It is conspicuous on account of the lack of ornamentation on its surface.

Tecnomorphs with a velar ridge (cf. Pl. VI, Fig. 8) which is usually distinct even in small specimens, occasionally, however, rounded, narrow, and bend-like in comparatively large specimens (cf. Pl. VI, Fig. 4). In posterior direction the velar ridge becomes obsolete already before reaching the mid-height of the valve. In anterior direction the velar structure can be followed up to the anterior cardinal corner.

Heteromorphs with a moderately broad, slightly convex, flange-like dolon broadest anteroventrally. Posteriorly the dolon decreases gradually in width, and becomes obsolete usually at about the same point as the velar ridge in tecnomorphs. Anteriorly the dolon ends rather abruptly ventrally of the longitudinal line through the middle of the preadductorial node. The anterodorsal extension of the dolon varies, the end of the dolon lying rather low ventrally in the holotype (cf. Thorslund 1940, Pl. 4, Fig. 8), and rather high dorsally in the specimen figured on Pl. VI, Fig. 6. The width and convexity of the dolon likewise show some variation comparable to that in some species of *Euprimites*. The contact area between the dolon and the domicilium lies highest upon the side of the valve anteroventrally, curving from this point rather steeply in anterodorsal and more gently in posterior direction down to the level of the tecnomorphic velar ridge. The lateral surface of the dolon is usually faintly undulate.

Both valves possess a distinct marginal ridge. On viewing closed carapaces from the ventral direction the marginal ridge of the left valve appears slightly broader and more protruding than that of the right valve (Pl. VI, Fig. 4).

In well-preserved specimens the whole lateral surface of the valve, except for the muscle scar and the adductorial node, is ornamented with a faint reticulation and rather small, scattered tubercles, arranged in an irregular row close to the dorsal margin. In less well preserved specimens the reticulation is scarcely visible, and the ornamentation then appears to consist of the tubercles only.

Dimensions.—See Table 15.

Table 15.

No.	Mus. cat. no.	L. valve	H. valve	H-L	Valve	Locality	Remarks
1	SGU	1.16	0.68	0.91	h—l	1.2 km W of Tandsbyn railway station	Holotype. THORSLUND 1940, Pl. 4, Fig. 8.
2	UM T 80	1.16	0.69	—	t—l	Ringsö, Tvären	Figured on Pl. VI, Fig. 9.
3	UM T 88	1.15	0.74	—	t—r	,, ,,	,, ,, Pl. VI, Figs. 7–8.
4	UM T 87	1.14	0.66	0.88	h—c	,, ,,	,, ,, Pl. VI, Fig. 6.
5	UM T 81	1.12	0.62	0.86	t—c	,, ,,	,, ,, Pl. VI, Fig. 4.
6	UM T 85	1.12	0.67	0.80	t—l	,, ,,	
7	UM T 82	1.10	0.66	0.78	t—r	,, ,,	
8	UM T 84	1.10	0.66	—	t—l	,, ,,	
9	UM T 79	0.99	0.60	—	t—r	,, ,,	Figured on Pl. VI, Fig. 5.
10	UM T 83	0.93	0.57	0.74	t—l	,, ,,	
11	UM T 86	0.91	0.53	—	t—l	,, ,,	

DISCUSSION.—The holotype has a shorter and more convex dolon than the heteromorphs studied from the Tvären area, but agrees with the material from Tvären in all details of ornamentation as well as in size.

T. granosa (ÖPIK) seems to be a very similar species, having the same outline and possessing a preadductorial node, and although the sulcus is missing according to ÖPIK (1937, p. 14), a slight sulcal depression can obviously be traced on Pl. XIII, Fig. 6 of his paper. The only clear difference between *T. carinata* and *T. granosa* seems to lie in the ornamentation, that of the latter species being tuberculate without reticulation. It is, however, not excluded that further examinations may reveal a faint reticulation also in well-preserved specimens of *T. granosa*, and in this case the two species might be conspecific. No material for comparison of *T. granosa* from Estonia has been at the present writer's disposal. The specimen figured by ÖPIK (1937) on Pl. XV, Fig. 7 as *Apatochilina ubjaensis* very likely is a heteromorphic valve of *T. granosa*, being very similar to the heteromorphs of *T. carinata*, except for the ornamentation. *Primitiella indistincta* ÖPIK may have been erected on young instars of *T. granosa*. Its holotype is only 0.8 mm long, thus probably an early instar, and the lack of a distinct ornamentation, as stated by ÖPIK (1937, p. 13), may be due to preservation. Without having studied the actual material the present author is, however, compelled to leave this question open. Both species have been regarded as conspecific by SARV (1956a, p. 51).

OCCURRENCE.—*T. carinata* has been found only in the *Ludibundus* limestone.

Jämtland, Brunflo-Lockne area. Exposure 1.2 km W of the Tandsbyn railway station. *Södermanland*, Tvären area. Ringsö (boulders).

Gen. *Euprimites* Hessland, 1949

Type Species.—*Euprimites reticulogranulatus* Hessland, 1949.

Diagnosis.—Unisulcate, sulcus relatively short, more or less straight or slightly curved, transversally directed, ventral part as a rule slightly expanded and mostly surrounded by a low horseshoe-shaped elevation. Hinge-line relatively long, dorsum comparatively low, epicline. Tecnomorphs with a narrow velar ridge at least in the adult stage, heteromorphs anteroventrally with a moderately broad, more or less convex dolon.

Species.—*Euprimites reticulogranulata* Hessland, 1949
Primitia bursa Krause, 1889
Primitia? *eutropis* Öpik, 1937
Euprimitia plena Öpik, 1937
Euprimitia(?) *locknensis* Thorslund, 1940
Euprimitia minor Thorslund, 1940
Ctenobolbina suecica Thorslund, 1940
? *Euprimitia tenuireticulata* Hessland, 1949
Euprimites bursellus n.sp.
Euprimites effusus n.sp.
Euprimites anisus n.sp.

Euprimitia tenuireticulata Hessland, 1949, has a shallower sulcus than the species referred here to *Euprimites*. It may belong to the same genus, but this cannot be ascertained before the species is not better known (only 3 tecnomorphic valves, partly fragmentary, known at present). The generic reference of the other small species referred by Hessland (1949) to *Euprimitia* cannot be decided at present, but they certainly do not belong to *Euprimitia*, as suggested also by Henningsmoen (1953a, p. 198); part of the described specimens may be rather early instars.

Euprimitia plena Öpik, 1937, also has a shallower sulcus than usual in *Euprimites*, and the heteromorphic type is unknown. The general shape of the tecnomorphic valves, agrees, however, rather closely with that of the other species of *Euprimites*, especially in respect to the development of the velar ridge. According to Sarv (1956a, p. 49) *Euprimitia bilabrata* Öpik, 1937, and *E.* sp. aff. *bilabrata* Öpik, 1937, are synonyms of *E. plena*.

Euprimitia buttsi Ulrich & Bassler, 1923b, has been tentatively referred to *Euprimites* by Hessland (1949, p. 250). To judge from the figures in Ulrich & Bassler (1923b, Pl. XXXVII, Figs. 1, 2) there certainly is an external resemblance between this species and *Euprimites*, but *E. buttsi* cannot be placed with certainty in any described genus as long as its dimorphism is unknown. Most probably this Lower Silurian species does not belong to *Piretellidae* at all and perhaps not even to *Eurychilinacea*.

poorly defined anteriorly, where it is marked only by a faint change in convexity. Posteriorly the dolon reaches to about the mid-length of the post-adductorial area. Farther in posterodorsal direction the velar structure is developed as a rounded ridge, and higher dorsally, close to the cardinal corner, as an indistinct bend. The anterodorsal end of the dolon reaches almost up to the anterior cardinal corner. The inner, plane part of the dolon shows a faint undulation.

The lateral surface of the domicilium is covered by minute closely spaced granules (too minute to be visible in the photographs at the magnification of × 25) and relatively large tubercles of somewhat varying size. The proximal, plane part of the dolon has the same ornamentation, except that the tubercles are only few in number. The minute granules are for the most part arranged in rows so as to give the ornamentation sometimes a very finely reticulate appearance.

Dimensions of the holotype.—Length of the valve 1.34 mm; height of the valve 0.95 mm; length of the lateral surface of the domicilium 1.20 mm; height of the lateral surface of the domicilium 0.73 mm.

Discussion.—As long as the development of the tecnomorphic velar structure is unknown the generic reference of this species is somewhat uncertain. As, however, the heteromorphs exhibit a close similarity to those of *P. geniculata* the species described belongs in all probability to *Piretia*.

The specimens figured by Krause (1891, Pl. XXXI, Figs. 6, 7) as *Primitia* aff. *Jonesii* Krause resemble the species described. The heteromorphic valve figured by him has also approximatively the same size (length 1.43 mm according to Krause 1891, p. 494) as that of *P. clypeolaria*. The sulcus is, however, slightly shorter in Krause's figures, and the details of the ornamentation cannot be compared, the figures of Krause being too schematical in this respect. The general appearance of the ornamentation is, however, closely similar. According to Krause the specimens figured by him were found in a grey "*Beyrichia*" limestone, and thus probably come from a higher stratigraphic horizon (*Schroeteri* limestone?) than *P. clypeolaria*. They may be conspecific with the latter species, but this cannot be proved at present.

Occurrence.—*Piretia clypeolaria* has been found so far only in the *Platyurus* limestone.

Öland.—Skärlöv bore (1 heterom.). *Östergötland*.—Motala bore (2 tecnom.).

Gen. *Uhakiella* Öpik, 1937

Type Species.—*Uhakiella coelodesma* Öpik, 1937.

Diagnosis.—Unisulcate, with a distinct adductorial pit. Some species with a flattened, indistinct ventral lobe, a ridge around the ventral part of the sulcus, and close to each cardinal corner with a low, rounded dorsal plica; other species without any conspicuous elevations on the lateral surface of the

domicilium. Tecnomorphs with a frill-like velar flange, velar ridge, or without a velar structure. Heteromorphs with a strongly convex velar dolon; the inner part of the lateral surface of the dolon lies almost at the same level as the general lateral surface of the domicilium, and has usually also the same type of ornamentation.

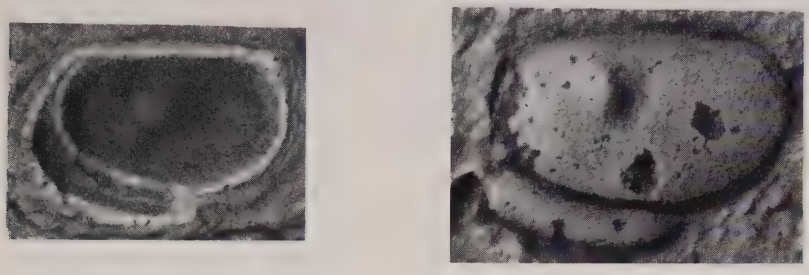
SPECIES.—*Beyrichia strangulata* SALTER, 1851.[1]
Beyrichia granulifera ULRICH & BASSLER, 1909
Uhakiella coelodesma ÖPIK, 1937
Uhakiella kohtlensis ÖPIK, 1937
Uhakiella pumila ÖPIK, 1937
Bromidella linnarssoni HENNINGSMOEN, 1948
Primitia osloensis HENNINGSMOEN, 1954
Uhakiella aequigranosa n.sp.
Uhakiella periacantha n.sp.

HENNINGSMOEN (1953b) included also *Eurychilina* [= *Actinochilina*] *suecica* THORSLUND, 1948, in *Primitia* (= *Uhakiella*) but this species is certainly an eurychilinid (cf. p. 258).

GENERIC CHARACTERS.—The outline of the species of *Uhakiella* varies from nearly amplete to rather strongly postplete. The adductorial pit is as a rule rather deep in its deepest part, its outline varies from rounded to oblong or quadrangular. The dorsum is low to moderately high, usually slightly epicline.

In several species the lateral surface of the domicilium shows a characteristic arrangement of lobes and ornamental ridges. Their general pattern has been represented diagrammatically by ÖPIK (1937, p. 43, Fig. 5). The ventral end of the adductorial pit is surrounded by a rounded horseshoe-shaped ridge, the anterodorsal end of which is expanded, and forms a more or less distinct preadductorial node ("node-like middle lobe" in ÖPIK loc. cit.). Posterodorsally the ridge merges into an indistinctly delimited, rather large elevation (= anterior lobe in ÖPIK, loc. cit.) which is, however, scarcely visible in most species. The horseshoe-like swelling is delimited ventrally by a faint depression, and ventrally of it the surface of the valve is inflated forming a flattened ventral

[1] It is difficult to ascertain the exact date of erection of this species. The species was described as "n.sp." by SALTER (1854, p. II, Pl. 1E, Figs. 1, 1a, 1b) in the Appendix A to "A Synopsis of the Classification of the British Palaeozoic Rocks" by SEDGWICK. The introduction of the Appendix is dated by SALTER Febr. 1852 indicating possibly the date when his manuscript was finished. On p. 136 of the "Synopsis" the species was redescribed by MCCOY who referred for the illustration to the plate in SALTER's Appendix. According to HILL (1938, p. 45) the page 136 of the "Synopsis" was published in 1851. If her dating is correct the redescription of the species by MCCOY appeared before the termination of SALTER's manuscript. MCCOY, however, clearly states that SALTER is the author of the species, and he also undoubtedly had access to SALTER's manuscript. Therefore, SALTER must be regarded as the author of the species, and if the description by MCCOY appeared in 1851, this date should be taken as the date of this species. The present writer is indebted to Dr. O. M. B. BULMAN for the information concerning the dating of different parts of the "Synopsis".



A B

Fig. 23. A, internal view of a right heteromorphic valve of *Uhakiella* cf. *coelodesma* Öpik. UM no. Vg. 88. Västergötland, Kinnekulle, Kullatorp core, 86.47 m. × 15. B, internal mould of a left heteromorphic valve of *Uhakiella strangulata* (Salter, 1851). SMC no. 29986. Coniston, Lancashire, probably Coniston limestone. Presumably one of the specimens figured by Salter 1854, Pl. 1E as *Beyrichia strangulata*. × 20.

lobe. Close to the anterior cardinal corner a more or less distinct ridge is developed (= posterior lobe in Öpik loc. cit.) which evidently corresponds to the anterior part of the dorsal plica in some other piretellids. Near the posterior cardinal corner the posterior part of the dorsal plica is occasionally present. Both arches of the dorsal plica are not connected in any species of *Uhakiella* hitherto described. The relief of the lateral surface of the domicilium of the type described above is most clearly expressed in *Uhakiella coelodesma*, *U. granulifera*, and *U. kohtlensis*, and very feebly developed, but discernible in *U. aequigranosa* and *U. periacantha*. In the other species of *Uhakiella* only the preadductorial node seems to be present.

Tecnomorphs of *U. strangulata* and *U. coelodesma* have a velar ridge, those of *U. kohtlensis* and *U. linnarssoni* a moderately wide velar flange which is frill-like in *U. kohtlensis*. *Uhakiella periacantha* does not seem to possess any tecnomorphic velar structure. In heteromorphs the dolon is always strongly convex, the contact area between the dolon and the domicilium placed high upon the side of the valve, lying anteroventrally at about the same general level as the lateral surface of the domicilium. The external boundary between the lateral surface of the dolon and that of the domicilium is as a rule fairly indistinct, in part owing to the usually identical ornamentation on both surfaces. No closed heteromorphic carapaces of *Uhakiella* have been found so far, but as the peripheral surface of the dolon is broad (tr.) and almost vertically directed the free edges of the dolon were apparently in contact in closed carapaces. The subvelar field of both valves possesses a ridge, but the exact position of these ridges as well as the closure of the carapace along the free edge are still incompletely known.

Discussion.—*Uhakiella* was by E. A. Schmidt (1941, p. 33) regarded as a junior subjective synonym of *Bromidella*. Henningsmoen (1948) and Thorslund (1948) joined this opinion. Later Henningsmoen (1953a, p. 226) considered "the strong dorsal ridge or rather swelling of *Bromidella* to be rather

unique", and concluded that it might be better to retain *Bromidella* as a separate genus. An examination of several specimens of the type species of *Bromidella* by the present writer has shown this genus to differ distinctly from *Uhakiella*. In *Bromidella reticulata* HARRIS (cf. Pl. IV, Fig. 23) the dorsum is fairly high (tr.) and strongly epicline. The dorsal plica is prominent, continuous along the whole dorsal margin, and its posterior part is thickened into a ventrally indistinctly delimited, mainly ornamental elevation. The preadductorial node is high and prominent. Also other species of *Bromidella* described by KAY (1940) possess these characters.

HENNINGSMOEN (1953a, b; 1954b) treated *Uhakiella* as very close to, or possibly identical with, *Primitia*. His definition of the latter genus was based on a re-examination of the type material of *Beyrichia strangulata* which species was designated as the type species of *Primitia* by MILLER (1889; cf. WARTHIN 1948, p. 645). As, however, an application will be submitted to the International Commission on Zoological Nomenclature for preserving the accustomed usage of the generic name *Primitia* (cf. p. 217) with *Primitia mundula* as the type species, this generic name will be transferred to a group of species of *Leperditellacea*. The type material of *Beyrichia strangulata* has been re-examined also by the present writer, and according to his observations there remains scarcely any doubt of this species belonging to a group of *Uhakiella* characterized by a narrow tecnomorphic velar ridge and by the absence of ornamental ridges or conspicuous elevations on the lateral surface of the domicilium. The type material of *U. strangulata* consists of internal moulds and external imprints, and the state of preservation is not especially favourable. Some of the specific characters are, therefore, incompletely known. The heteromorphs (Fig. 23B; cf. also the diagrammatic reconstruction by HENNINGSMOEN 1953a, p. 225, Fig. 11b) possess a strongly convex dolon. The ornamentation consists of fairly large scattered tubercles. The length of the heteromorphic valves slightly exceeds 2 mm. Without examination of a better preserved material of *U. strangulata*, it will, however, be difficult to distinguish this species from other species of the same group of *Uhakiella* with about the same type of ornamentation.

OCCURRENCE.—The earliest species of *Uhakiella* known so far appears in the Lasnamäe Stage (Lower Llandeilo) of Estonia (cf. SARV 1956a). No Silurian species referable to this genus are known. Hitherto the genus is unknown outside Europe.

Uhakiella cf. *coelodesma* ÖPIK, 1937

Pl. V, Figs. 6–9; Text-fig. 23A.

cf. 1937 *Uhakiella coelodesma* n.sp.—ÖPIK, pp. 43–44, Pl. III, Figs. 1–3.
1940 *Uhakiella coelodesma* ÖPIK—THORSLUND, p. 172, Pl. I, Figs. 6, 7.
1948 Bromidella coelodesma (ÖPIK)—THORSLUND, pp. 350, 359.

DESCRIPTION.—The following description of the tecnomorphs is based upon the specimens from the Tvären area, and that of the heteromorphs upon speci-

mens from the Kullatorp core. In the boulders of the Tvären area no heteromorphs have been found so far, and in the bores of Västergötland all tecnomorphs are poorly preserved.

Adductorial pit relatively large, somewhat quadrangular in outline, surrounded ventrally and anteriorly by a distinct rounded ridge, which culminates anterodorsally in a low node and posteriorly in a poorly defined inflation. Dorsally of the adductorial pit the surface of the valve is faintly depressed. A broad, shallow depression is developed ventrally of the horseshoe-shaped ridge. Ventrally from this depression the ventral part of the lateral surface of the domicilium is faintly inflated forming a flattened ventral lobe. A rather distinct anterior arch of the dorsal plica is situated close to the anterior cardinal corner, and on some specimens from the Tvären area a corresponding plica is developed also posteriorly. The posterior arch of the dorsal plica is always lower and less distinct than the anterior arch. The peripheral part of the lateral surface of the domicilium is usually rather distinctly flattened ventrally of the ventral lobe in tecnomorphs.

Tecnomorphs with a narrow, rounded, bend-like velar ridge. Right valve with an admarginal ridge fairly close to the velar ridge, the left valve with a marginal ridge close to the free edge. The ridges on the subvelar field of both valves have a row of spines (cf. THORSLUND 1940, Pl. 1, Figs. 6, 7) which, however, are often broken off. The ridges then appear to bear a row of tubercles (cf. Pl. V, Fig. 8). The actual closure of the carapace was not observed, but evidently the left valve overlaps the right one along the free edge.

Dolon strongly convex, rather broad, anterior end reaching up to about the longitudinal line through the middle of the adductorial pit, posterior end to about the anterior third of the postadductorial area. Externally there is no distinct boundary between the dolon and the lateral surface of the domicilium.

The ornamentation consists of closely spaced tubercles, relatively large on the inflations and small in the depressions. The tubercles continue also upon the inner part of the lateral surface of the dolon. In all examined specimens from the Tvären area and from Östergötland the tubercles are lower and more indistinct than in those from Västergötland.

DIMENSIONS.—See Table 13.

DISCUSSION.—The specimens described are very similar to *Uhakiella coelodesma* ÖPIK, and no definite differences can be pointed out. There may, however, exist differences in the ornamentation as this cannot be observed clearly enough on ÖPIK's (1937, Pl. III, Figs. 1–3) figures, and since no Estonian material has been at the author's disposal for comparison, it is safer at the time being not to attempt a definite identification. The Swedish material also occurs in a slightly higher stratigraphical horizon than the Estonian. The differences, if present, are, however, probably of merely subspecific value. On the other hand, the possibility must be taken into account that the differences in ornamentation between the specimens from Västergötland and those from

Table 13.

No.	Mus. cat. no.	L. valve	H. valve	L. domic.	H-L	Valve	Locality	Remarks
1	UM Vg. 87	2.55	1.69	2.40	—	h—l	Kullatorp 86.47 m	Figured on Pl. V, Fig. 6.
2	UM Vg. 88	2.37	1.59	—	1.53	h—r	,, ,, ,,	
3	UM T 5	1.78	1.11	—	1.31	t—r	Tvären, Ringsö	Thorslund 1940, Pl. 1, Fig. 6.
4	UM T 6	1.76	1.11	—	1.33	t—l	,, ,,	Thorslund 1940, Pl. 1, Fig. 7.
5	UM T 95	1.51	0.95	—	1.13	t—r	,, ,,	Figured on Pl. V, Figs. 7–8.
6	SGU	1.22	0.79	—	—	t—r	Smedsby Gård 96.37 m	Figured on Pl. V, Fig. 9.

the other districts might indicate the presence of two different species or subspecies also in Sweden.

The specimen of *Bollia granulosa* Krause figured by Krause (1889) on Pl. II, Fig. 1 was referred by Öpik (1937, p. 43) to *U. coelodesma*. The figure by Krause shows, however, a rather different ornamentation, and the reference is, therefore, highly uncertain. Also *Primitia* aff. *Jonesi* Krause, figured by Krause 1891, Pl. XXXI, Fig. 6 was referred by Öpik (loc. cit.) to this species. But, as pointed out by Thorslund (1940, p. 172) this is not a likely assumption. In the present writer's opinion this specimen figured by Krause probably belongs to *Piretia* (cf. p. 285).

Occurrence.—*Uhakiella* cf. *coelodesma* has been found in Sweden only in the lower part of the *Ludibundus* beds. In Estonia *U. coelodesma* occurs according to Sarv (1956a, p. 53) in the Lasnamäe Stage (C_1b) and in the lower part of the Uhaku Stage (C_1c). Its occurrence in C_1b needs, however, further confirmation.

Södermanland, Tvären area, erratic boulders (3 tecnom.). *Öland*.—Böda Hamn bore (2 tecnom.). *Östergötland*.—Smedsby Gård bore (2 heterom., 2 tecnom.). *Västergötland*, Kinnekulle.—Kullatorp bore (2 heterom., 1 tecnom.); Norra Skagen bore (2 heterom., 1 tecnom.).

Uhakiella aequigranosa n. sp.

Pl. V, Figs. 10–11.

Holotype.—Left heteromorphic valve, UM no. D 427, figured on Pl. V, Fig. 10.

Type Locality.—Fjäcka, locality no. 4 (cf. Jaanusson 1947, p. 44, Fig. 2).

Type Stratum.—Uppermost *Crassicauda* limestone.

Derivation of the Name.—The name refers to the ornamentation which consists of tubercles of about uniform size.

DIAGNOSIS.—Length of the heteromorphs about 2,1 mm. Ornamental ridges very faint, scarcely discernible. No distinct external boundary between dolon and domicilium. In posterior direction the dolon reaches to about the mid-length of the postadductorial area. Surface ornamented with relatively large, closely spaced tubercles of about uniform size all over the lateral surface of the domicilium and the inner part of the lateral surface of the dolon.

DESCRIPTION.—Outline almost amplete to slightly preplete. Lateral surface of the domicilium rather faintly convex, highest convexity somewhat behind the adductorial pit. Adductorial pit oblong, of moderate size, surrounded, except dorsally, by a poorly defined, scarcely discernible, horseshoe-shaped ridge, the anterodorsal end of which terminates in an indistinct, flattened preadductorial node. A very indistinct and faint trace of a dorsal plica can be observed near the anterior cardinal corner.

In tecnomorphs the details of the peripheral part of the valve have not been accessible to clear observation, it proving very difficult to clean the specimens from a hard matrix. No velar structure seems, however, to exist or perhaps only a very faint velar ridge.

In the heteromorphs the dolon is anteroventrally strongly convex, pouch-like. The anterodorsal end of the dolon reaches to about the longitudinal line through the middle of the preadductorial pit or slightly farther in dorsal direction. The posterior end reaches to about the mid-length of the post-adductorial area. Externally no distinct boundary is present between the lateral surface of the domicilium and the inner part of the dolon.

The ornamentation consists of relatively large, closely spaced tubercles of about uniform size all over the lateral surface of the valve and the inner part of the dolon. The diameter of the tubercles much exceeds the distance between the tubercles.

DIMENSIONS.

	Left heteromorphic valve. Holotype	Right tecnomorphic valve. Figured on Pl. V, Fig. 11
Length of the valve	2.10	1.27
Height of the valve	1.46	0.82

DISCUSSION.—By its ornamentation and the indistinct ornamental ridges *U. aequigranosa* differs clearly from other species of *Uhakiella* from Balto-scandia. The arrangement of the ridges is on the whole identical with that in *U. coelodesma*, but the ridges are very faint. The ornamentation of *U. aequigranosa* resembles to a certain extent that of *U. strangulata*. In the latter species, however, the tubercles are not so closely spaced as in *U. aequigranosa*, the distance between the tubercles being usually twice the diameter of tubercles or greater.

Occurrence.—*Uhakiella aequigranosa* n.sp. has only been found in the *Crassicauda* limestone of Sweden.

Siljan district, Dalarna.—Fjäcka (1 heterom., 1 tecnom.). *Öland.*—Gammalsby bore (1 heterom., 3 tecnom.). *Östergötland.*—Motala bore (2 tecnom.).

Uhakiella periacantha n. sp.

Pl. V, Figs. 12–17; Text-figs. 6, 24, 25.

Holotype.—Left heteromorphic valve, UM no. B 211, figured on Pl. V, Figs. 13–14.

Type Region.—South Bothnian area. The holotype was found in the erratic boulder Bergsbrunna no. 1.

Type Stratum.—Uppermost beds of the *Crassicauda* limestone.

Derivation of the Name.—The name refers to the marginal spines along the entire free margin.

Diagnosis.—Length of the heteromorphs (excluding the marginal spines) 1.15–1.30 mm. Nodes and ridges very faintly developed. Tecnomorphs with-

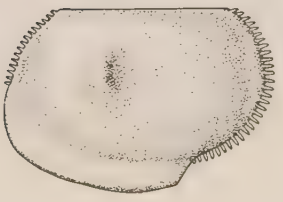


Fig. 24. Reconstruction of a heteromorphic valve of *Uhakiella periacantha* n.sp. Number and size of the marginal spines are approximative. ×40.

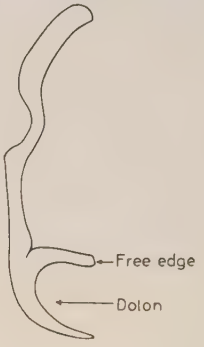


Fig. 25. *Uhakiella periacantha* n.sp. Diagrammatic drawing of a transversal section of a heteromorph. After a thin section, cf. Pl. XIV, Fig. 2. × 50.

out velar structure. Boundary between lateral surface of the dolon and that of the domicilium marked by a shallow furrow. The posterior end of the dolon reaches to about the mid-length of the postadductorial area. Marginal spines along whole length of the free edge. The ornamentation consists of minute, closely spaced tubercles. Their diameter is usually about equal to the distance between the tubercles. Dolon with faint radial striation.

Material.—11 heteromorphic, 20 tecnomorphic valves.

Description.—Domicilial outline slightly postplete or nearly amplete; highest convexity somewhat behind the adductorial pit. Dorsum low, slightly epicline. Adductorial pit of varying size, sometimes rather small (Pl. V, Fig. 13), occasionally also moderately large (Pl. V, Fig. 15), oblong. The pit is sur-

Table 14.

No.	UM Mus. cat. no.	L. valve	H. valve	L. domic.	H. domic.	H-L	Valve	Remarks
1	B 223	1.28	0.91	1.19	0.75	—	h—l	
2	B 216	1.24	0.88	1.16	—	0.76	h—l	
3	B 229	1.24	0.82	1.16	0.68	0.68	h—l	
4	B 228	—	0.84	—	0.68	—	h—r	
5	B 211	1.24	0.86	1.15	0.69	0.76	h—l	Holotype. Pl. V, Figs. 13–14.
6	B 212	1.24	0.87	1.15	0.71	—	h—l	Figured on Pl. V, Fig. 15.
7	B 213	1.20	0.83	1.13	0.69	0.72	h—r	,, ,, Pl. V, Figs. 16–17.
8	B 230	1.16	0.79	1.11	0.66	0.76	h—r	
9	B 220	1.04	0.69	—	—	—	t—l	
10	B 226	1.03	0.70	—	—	0.70	t—l	Figured on Pl. V, Fig. 12.
11	B 219	1.03	0.69	—	—	—	t—l	
12	B 218	1.00	0.67	—	—	—	t—l	
13	B 227	0.88	0.57	—	—	0.61	t—l	
14	B 222	0.88	0.57	—	—	0.64	t—l	
15	B 224	0.87	0.56	—	—	0.61	t—r	
16	B 285	0.86	0.55	—	—	—	t—r	
17	B 215	0.82	0.56	—	—	0.60	t—l	
18	B 217	0.77	0.51	—	—	0.58	t—l	
19	B 214	0.74	0.50	—	—	—	t—l	
20	B 221	0.72	0.48	—	—	0.53	t—r	
21	B 225	0.70	0.47	—	—	—	t—r	

rounded, except dorsally, by a low and indistinct horseshoe-shaped ridge with the anterodorsal end culminating in a low poorly defined node. Anteroventrally of the horseshoe-shaped ridge the surface of the domicilium is faintly depressed. A faint trace of a dorsal plica near the anterior cardinal corner, no such trace posteriorly.

In tecnomorphs no trace of a velar structure has been observed. Dolon strongly convex, peripheral part steeply sloping. The anterior end of the dolon reaches to about the longitudinal line through the middle of the preadductorial pit, the posterior end to about the mid-length of the postadductorial area. The boundary between the dolon and the domicilium is marked externally by a shallow, indistinct furrow, or, rather, a faint change in convexity.

A row of marginal spines is developed along the whole free margin. The width of each spine is about equal to the distance between the spines, and the length of each spine seems usually to be about twice the width. The spines were, however, as a rule rather badly preserved, and the above data about their proportions are only approximative.

The ornamentation of the lateral surface of the domicilium consists of minute, closely spaced tubercles, the diameter of the tubercles being roughly equal to the distance between the tubercles. The tubercles continue also on

the proximal part of the dolon, but are smaller there. The dolon carries, furthermore, a faint radial striation.

Dimensions.—See Table 14. In measuring the length and the height of the valve the marginal spines have been excluded.

Discussion.—By its small size and by its ornamentation *U. periacantha* differs distinctly from the other species of *Uhakiella* described so far. The most closely similar species seems to be *U. pumila* Öpik which according to Öpik's figure (1937, Pl. III, Fig. 5) has also a similar row of marginal spines. In *U. pumila*, however, according to the figure of the holotype in Öpik (1937) the adductorial pit has a slightly more dorsal position, and is rather indistinctly delimited dorsally, thus resembling a short sulcus. Moreover, the dolon is considerably shorter.

Occurrence.—*Uhakiella periacantha* n.sp. has been found only in the South Bothnian erratic boulder Bergsbrunna no. 1 in which it is a rather common species.

Subfam. TVAERENELLINAE nov.

Diagnosis.—Dolon faintly to moderately convex, its peripheral edges not in contact in closed carapaces, but separated by a broad or moderately broad space.

Genera.—*Dicranella* Ulrich, 1894
? *Ectoprimitia* Bouček, 1936
Hesperidella Öpik, 1937
Euprimites Hessland, 1949
Tvaerenella n.gen.
Levisulculus n.gen.

Discussion.—This subfamily consists of two rather distinct groups of genera, one of them including *Hesperidella* and *Dicranella*, and the other the remaining genera. There is scarcely any doubt that the genera within each group are closely related. The main difference between the groups lies in the shape of the preadductorial node which is developed as a knob or spine in the *Hesperidella* group, but as a flattened and often indistinct node in the *Tvaerenella* group. The possibility of expressing the difference between these groups also in the classification has been considered. No step in this direction has, however, been found advisable for the time being, mainly on account of difficulties in formulating sufficiently sharp diagnoses. The shape of the dolon is very similar in both groups, but may have originated independently along two different lines. In order to answer this question more species of both groups will have to be studied. The *Hesperidella* group resembles the *Piretellinae* more than does the *Tvaerenella* group, and is apparently more closely related to it. *Parabolbina*

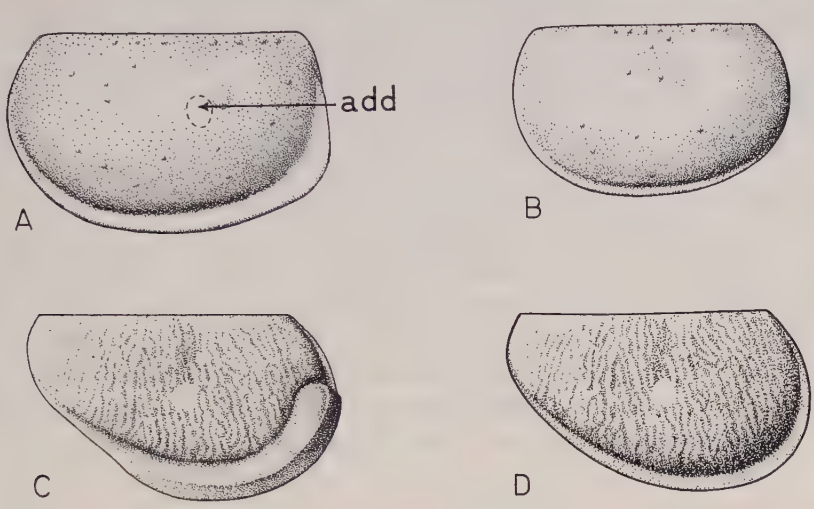


Fig. 26. Reconstructions of (A, B) *Tvaerenella carinata* (THORSL.) and (C, D) *Levisulculus lineatus* n.sp. × 35. *add* = the position of the scar of the adductor muscle. To the left heteromorphs (A, C), to the right tecnomorphs (B, D).

staufferi KAY, 1940, (if erected on heteromorphs) and *Parabolbina carinifera* KAY, 1940, (if erected on tecnomorphs) seem to belong to the *Hesperidella* group of *Tvaerenellinae*. As pointed out also by HENNINGSMOEN (1953a, p. 239) they have certainly nothing in common with *Parabolbina*. If the interpretation of their probable dimorphism as given above is correct, a new genus must be erected for their inclusion. Representatives of one or two further new genera of the *Tvaerenella* group have been examined by the present writer, but their description lies outside the scope of the present paper.

The type species of *Ectoprimitia* BOUČEK, 1936, may be a member of the *Tvaerenellinae* of the *Tvaerenella* group. As, however, the type species, *Primitia corrugata* KRAUSE, 1892, is poorly known (the specimen figured by KRAUSE 1892 being the only one found by him and, moreover, apparently lost) the genus can hardly be characterized at present. HESSLAND (1949, pp. 224–225) considered *Ectoprimitia* to be similar to *Primitiella* from which it differs, in his opinion, by a deeper, narrower, and more dorsally extending sulcus. According to his interpretation the flange along the free margin in *Primitia corrugata* KRAUSE, 1892, is a depressed marginal zone, and not a velar structure. It is, however, difficult to see why HESSLAND considered the "Saum" (KRAUSE 1892, p. 386) in this species to be a marginal structure, the present writer is inclined to regard it as a narrow velar flange similar to that in tecnomorphs of *Levisulculus*. According to the latter interpretation *Ectoprimitia tenuireticulata* HESSLAND, 1949, is not an *Ectoprimitia*, but belongs somewhere in the proximity of *Primitiella*. *Ectoprimitia corrugata krausei* BOUČEK, 1936, occurs in much younger strata (Ludlow, $e\beta$, cf. BOUČEK 1936, p. 45) than the type species, and

as long as it is not known whether or not it possessed a velar dimorphism, the generic reference is highly uncertain.

Occurrence.—The earliest *Tvaerenellinae* known so far appear in the "*Raniceps*" limestone of Baltoscandia (*Euprimites*, *Tvaerenella*).

Gen. *Tvaerenella* n. gen.

Type Species.—*Primitiella carinata* Thorslund, 1940.

Derivation of the Name.—After the Tvären area in which the type species is occasionally rather common.

Diagnosis.—No sulcus or merely a faint sulcal depression. A moderately large large muscle scar is situated somewhat dorsally of the mid-height of the lateral surface of the domicilium. Tecnomorphs with a more or less distinct velar ridge; heteromorphs with a usually rather long, slightly convex, flange-like dolon, broadest anteroventrally.

Species.—*Primitiella*? *carinata* Thorslund, 1940
Primitiella granosa Öpik, 1937
? *Primitiella pulex* Öpik, 1937
Apatochilina ubjaensis Öpik, 1937
? *Primitiella magna* Sarv, 1956
? *Primitiella longa* Sarv, 1956.

According to Sarv (1956a, p. 51) *Primitiella indistincta* Öpik, 1937, is conspecific with *P. granosa*. *Apatochilina ubjaensis* is based most probably on heteromorphs of a species of *Tvaerenella* (cf. p. 299). *Primitiella pulex* Öpik has an outline rather different from the other species referred here to *Tvaerenella* reminding in this respect of *Levisulculus*, and as long as the heteromorphs and the location of the muscle scar are unknown, this species can only tentatively be referred to *Tvaerenella* (cf. also p. 322). The published figures of "*Primitiella*" *magna* and "*P.*" *longa* are too poor for a safe generic reference of these species.

Generic Characters.—The genus *Tvaerenella* can be best characterized as an *Euprimites* without sulcus or with merely a faint sulcal depression. In other characters this genus is very similar to *Euprimites*. "*Euprimitia*" *plena* Öpik seems to occupy a somewhat intermediate position between *Tvaerenella* and *Euprimites*, but by its rather narrow, though shallow, sulcus stands apparently closer to the latter genus.

Within the genus *Tvaerenella* as defined in the present paper, forms without any trace of a sulcus, like *T. pulex*, as well as species with a rather distinct, but poorly defined sulcal depression are united. Both these types seem to be joined by a morphological series which in this respect is rather continuous. In front of the sulcal depression a small, low presulcate node can be developed, and posteroventrally of the node a rounded, smooth muscle scar can usually

be distinguished. The latter is situated dorsally of the mid-height of the domicilium (Fig. 26 A) and thus has a position closer to the dorsal margin than that of *Levisulculus*. The dorsum is rather low, almost orthocline to slightly epicline.

Tecnomorphs with a velar ridge, resembling that of *Euprimites*. This ridge may, however, be weak and bend-like even in rather late instars. The dolon in heteromorphs is moderately broad, slightly convex, and flange-like, resembling that of *Euprimites*. The contact area between the dolon and the domicilium is placed rather considerably higher upon the side of the domicilium than that between the corresponding part of the velar structure and the domicilium in the tecnomorphs. At present the dimorphism is known only in the type species.

Upon the subvelar field both valves carry a strong ridge. As in *Euprimites* the marginal ridge of the left valve is as a rule slightly stronger than that of the right valve (cf. Pl. VI, Fig. 4; Öpik 1937, Pl. XIII, Fig. 9). The left valve seems to overlap the right valve to some extent along the free margin, but the details of the overlap have so far not been accessible to investigation.

Discussion.—Formerly the species included here in *Tvaerenella* have generally been placed in *Primitiella*. The latter genus is, however, non-velate, and belongs to quite a different group of palaeocope ostracodes.

Occurrence.—The earliest species of *Tvaerenella* known to the present writer occurs in the "*Raniceps*" beds of Western Estonia. In a piece of Pakri calcareous sandstone from the Island of Väike Pakri (Lilla Rågö) collected by G. Holm (RM no. Ar. 30002) the present writer has found a heteromorphic valve which evidently belongs to *Tvaerenella*. The other species known at present come from the Middle Ordovician and the lowermost Upper Ordovician. Outside Baltoscandia the genus is unknown.

Tvaerenella carinata (Thorslund, 1940)

Pl. VI, Figs. 4–9; Text-fig. 26 A–B.

1940 *Primitiella ? carinata* n.sp.—Thorslund, p. 163, Pl. 4, Fig. 8.

Holotype.—Left heteromorphic valve figured by Thorslund 1940, Pl. 4, Fig. 8 (SGU).

Type Locality.—Exposure 1.2 km W of the Tandsbyn railway station, Brunflo-Lockne area, Jämtland.

Type Stratum.—Lower *Ludibundus* limestone.

Diagnosis.—Length of heteromorphs 1.10–1.20 mm. Outline nearly amplete. Domicilium with an indistinct sulcal depression and with a small, flattened preadductorial node in front of it. Ornamentation consisting of a faint reticulation and scattered, rather small tubercles.

Material.—5 heteromorphic and 15 tecnomorphic valves and carapaces.

Description.—Outline nearly amplete or faintly postplete, domicilium rather strongly and more or less regularly convex. The highest convexity lies

slightly behind the sulcal depression, somewhat ventrally of the middle of the valve. The length and convexity of the valves vary rather considerably as also observed by Öpik (1937, p. 14) in *T. granosa*. Dorsum moderately high, almost orthocline, its lateral margin formed usually by a sharp edge which in some specimens is slightly raised and ridge-like. The surface ventrally of the edge usually carries an irregular row of tubercles.

In front of the mid-length of the domicilium the surface is slightly depressed, forming a faint, poorly defined sulcal depression. In front of the depression the surface is slightly elevated forming a low, flattened preadductorial node which is scarcely discernible in some specimens. The area posteroventrally of the preadductorial node carries a rounded, moderately large adductorial muscle scar, situated slightly dorsally of the mid-length of the domicilium (Fig. 26 A). It is conspicuous on account of the lack of ornamentation on its surface.

Tecnomorphs with a velar ridge (cf. Pl. VI, Fig. 8) which is usually distinct even in small specimens, occasionally, however, rounded, narrow, and bend-like in comparatively large specimens (cf. Pl. VI, Fig. 4). In posterior direction the velar ridge becomes obsolete already before reaching the mid-height of the valve. In anterior direction the velar structure can be followed up to the anterior cardinal corner.

Heteromorphs with a moderately broad, slightly convex, flange-like dolon broadest anteroventrally. Posteriorly the dolon decreases gradually in width, and becomes obsolete usually at about the same point as the velar ridge in tecnomorphs. Anteriorly the dolon ends rather abruptly ventrally of the longitudinal line through the middle of the preadductorial node. The anterodorsal extension of the dolon varies, the end of the dolon lying rather low ventrally in the holotype (cf. Thorslund 1940, Pl. 4, Fig. 8), and rather high dorsally in the specimen figured on Pl. VI, Fig. 6. The width and convexity of the dolon likewise show some variation comparable to that in some species of *Euprimites*. The contact area between the dolon and the domicilium lies highest upon the side of the valve anteroventrally, curving from this point rather steeply in anterodorsal and more gently in posterior direction down to the level of the tecnomorphic velar ridge. The lateral surface of the dolon is usually faintly undulate.

Both valves possess a distinct marginal ridge. On viewing closed carapaces from the ventral direction the marginal ridge of the left valve appears slightly broader and more protruding than that of the right valve (Pl. VI, Fig. 4).

In well-preserved specimens the whole lateral surface of the valve, except for the muscle scar and the adductorial node, is ornamented with a faint reticulation and rather small, scattered tubercles, arranged in an irregular row close to the dorsal margin. In less well preserved specimens the reticulation is scarcely visible, and the ornamentation then appears to consist of the tubercles only.

Dimensions.—See Table 15.

Table 15.

No.	Mus. cat. no.	L. valve	H. valve	H-L	Valve	Locality	Remarks
1	SGU	1.16	0.68	0.91	h—l	1.2 km W of Tandsbyn railway station	Holotype. THORSLUND 1940, Pl. 4, Fig. 8.
2	UM T 80	1.16	0.69	—	t—l	Ringsö, Tvären	Figured on Pl. VI, Fig. 9.
3	UM T 88	1.15	0.74	—	t—r	,, ,,	,, ,, Pl. VI, Figs. 7–8.
4	UM T 87	1.14	0.66	0.88	h—c	,, ,,	,, ,, Pl. VI, Fig. 6.
5	UM T 81	1.12	0.62	0.86	t—c	,, ,,	,, ,, Pl. VI, Fig. 4.
6	UM T 85	1.12	0.67	0.80	t—l	,, ,,	
7	UM T 82	1.10	0.66	0.78	t—r	,, ,,	
8	UM T 84	1.10	0.66	—	t—l	,, ,,	
9	UM T 79	0.99	0.60	—	t—r	,, ,,	Figured on Pl. VI, Fig. 5.
10	UM T 83	0.93	0.57	0.74	t—l	,, ,,	
11	UM T 86	0.91	0.53	—	t—l	,, ,,	

DISCUSSION.—The holotype has a shorter and more convex dolon than the heteromorphs studied from the Tvären area, but agrees with the material from Tvären in all details of ornamentation as well as in size.

T. granosa (ÖPIK) seems to be a very similar species, having the same outline and possessing a preadductorial node, and although the sulcus is missing according to ÖPIK (1937, p. 14), a slight sulcal depression can obviously be traced on Pl. XIII, Fig. 6 of his paper. The only clear difference between *T. carinata* and *T. granosa* seems to lie in the ornamentation, that of the latter species being tuberculate without reticulation. It is, however, not excluded that further examinations may reveal a faint reticulation also in well-preserved specimens of *T. granosa*, and in this case the two species might be conspecific. No material for comparison of *T. granosa* from Estonia has been at the present writer's disposal. The specimen figured by ÖPIK (1937) on Pl. XV, Fig. 7 as *Apatochilina ubjaensis* very likely is a heteromorphic valve of *T. granosa*, being very similar to the heteromorphs of *T. carinata*, except for the ornamentation. *Primitiella indistincta* ÖPIK may have been erected on young instars of *T. granosa*. Its holotype is only 0.8 mm long, thus probably an early instar, and the lack of a distinct ornamentation, as stated by ÖPIK (1937, p. 13), may be due to preservation. Without having studied the actual material the present author is, however, compelled to leave this question open. Both species have been regarded as conspecific by SARV (1956a, p. 51).

OCCURRENCE.—*T. carinata* has been found only in the *Ludibundus* limestone.

Jämtland, Brunflo-Lockne area. Exposure 1.2 km W of the Tandsbyn railway station. *Södermanland*, Tvären area. Ringsö (boulders).

Gen. *Euprimites* Hessland, 1949

Type Species.—*Euprimites reticulogranulatus* Hessland, 1949.

Diagnosis.—Unisulcate, sulcus relatively short, more or less straight or slightly curved, transversally directed, ventral part as a rule slightly expanded and mostly surrounded by a low horseshoe-shaped elevation. Hinge-line relatively long, dorsum comparatively low, epicline. Tecnomorphs with a narrow velar ridge at least in the adult stage, heteromorphs anteroventrally with a moderately broad, more or less convex dolon.

Species.—*Euprimites reticulogranulata* Hessland, 1949
Primitia bursa Krause, 1889
Primitia? eutropis Öpik, 1937
Euprimitia plena Öpik, 1937
Euprimitia(?) *locknensis* Thorslund, 1940
Euprimitia minor Thorslund, 1940
Ctenobolbina suecica Thorslund, 1940
? *Euprimitia tenuireticulata* Hessland, 1949
Euprimites bursellus n. sp.
Euprimites effusus n. sp.
Euprimites anisus n. sp.

Euprimitia tenuireticulata Hessland, 1949, has a shallower sulcus than the species referred here to *Euprimites*. It may belong to the same genus, but this cannot be ascertained before the species is not better known (only 3 tecnomorphic valves, partly fragmentary, known at present). The generic reference of the other small species referred by Hessland (1949) to *Euprimitia* cannot be decided at present, but they certainly do not belong to *Euprimitia*, as suggested also by Henningsmoen (1953a, p. 198); part of the described specimens may be rather early instars.

Euprimitia plena Öpik, 1937, also has a shallower sulcus than usual in *Euprimites*, and the heteromorphic type is unknown. The general shape of the tecnomorphic valves, agrees, however, rather closely with that of the other species of *Euprimites*, especially in respect to the development of the velar ridge. According to Sarv (1956a, p. 49) *Euprimitia bilabrata* Öpik, 1937, and *E.* sp. aff. *bilabrata* Öpik, 1937, are synonyms of *E. plena*.

Euprimitia buttsi Ulrich & Bassler, 1923b, has been tentatively referred to *Euprimites* by Hessland (1949, p. 250). To judge from the figures in Ulrich & Bassler (1923b, Pl. XXXVII, Figs. 1, 2) there certainly is an external resemblance between this species and *Euprimites*, but *E. buttsi* cannot be placed with certainty in any described genus as long as its dimorphism is unknown. Most probably this Lower Silurian species does not belong to *Piretellidae* at all and perhaps not even to *Eurychilinacea*.

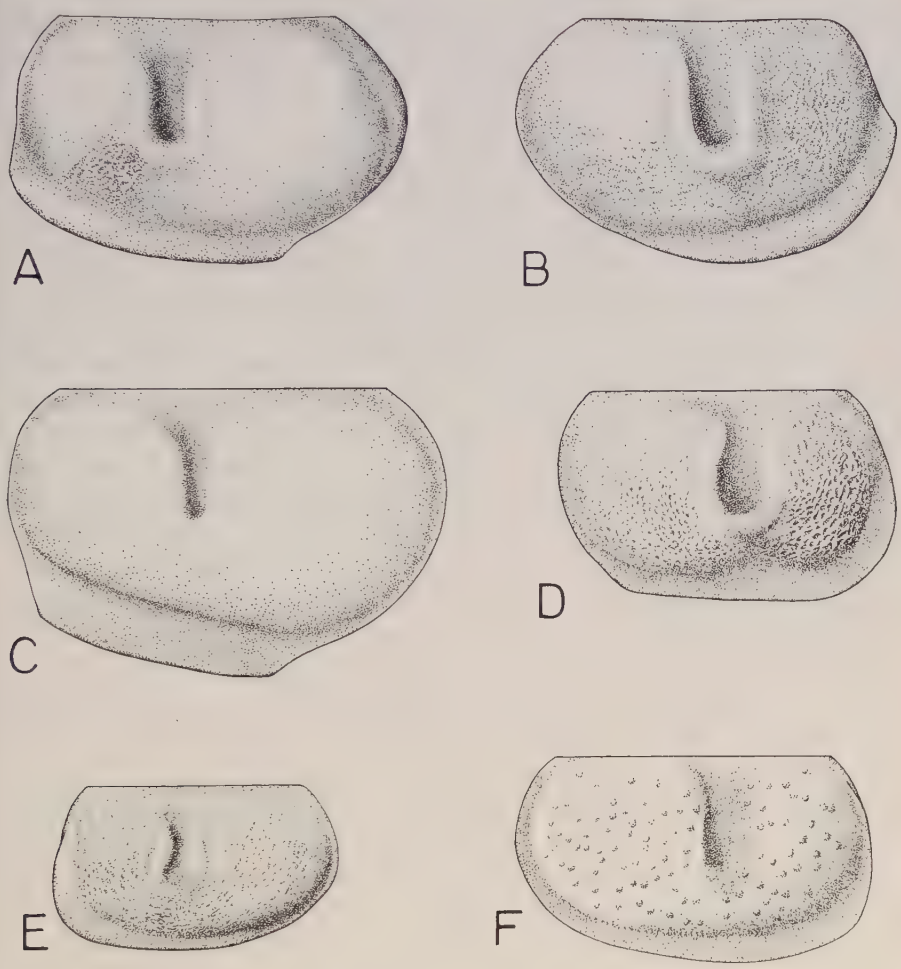


Fig. 27. Reconstructions of heteromorphic valves of some species of *Euprimites*. A, *Euprimites effusus* n.sp.; B, *Euprimites anisus* n.sp.; C, *Euprimites suecicus* (THORSLUND); D, *Euprimites locknensis* (THORSLUND); E, *Euprimites bursellus* n.sp.; F, *Euprimites eutropis* (ÖPIK) after the figure of the holotype (ÖPIK 1937, Pl. XIII, Fig. 2). Magnification ca. × 33.

GENERIC CHARACTERS.—The domicilial outline in the species of *Euprimites* described here is as a rule slightly postplete, in some species, as for instance in *E. suecicus*, even rather strongly postplete (cf. e.g. Pl. VIII, Figs. 1, 10). The velar structure is usually broadest anteroventrally, protrudes beyond the free edge, and thus often changes the lateral outline to nearly amplete or, in some species, even to slightly preplete.

The sulcus is deepest in its ventral part. Dorsally it becomes gradually shallower, and before reaching the hinge-line merges into the general lateral surface of the domicilium. The sulcus can thus also be described as a transversally oblong pit, deepest ventrally. It is usually more or less straight or, as in *E. bur-*

sellus, with a faint anteroventral curve of the ventral end. The ventral part of the sulcus is mostly surrounded by a more or less distinct elevation, sometimes developed as a horseshoe-shaped ridge. In some species, as in *E. suecicus* and *E. minor*, only a hardly recognizable trace of the elevation is present. Anteroventrally of the horseshoe-shaped elevation the lateral surface of the valve is often slightly depressed, as a rule more distinctly in the heteromorphs than in tecnomorphs.

Hinge-line comparatively long, dorsum rather low, as a rule epicline. In some species, as for instance in *E. effusus* (cf. Pl. VI, Fig. 12), the dorsum protrudes considerably beyond the hinge-line; in some other species, as for instance in *E. suecicus* (cf. Pl. VIII, Fig. 3), the dorsum is very low, and in strictly lateral view hardly conceales the hinge-line.

Tecnomorphs with a narrow velar ridge which may be present already in comparatively young instars, as in *E. effusus*, or may appear first in late instars, as in *E. suecicus*. Undescribed material of a new species of *Euprimites* seems to indicate that the tecnomorphs may even lack velar structure. Heteromorphs with a distinct dolon, the velar structure being anteroventrally expanded into moderately broad, more or less convex flange. The contact area between the dolon and the domicilium is placed as a rule considerably more dorsally than that between the corresponding part of the velar ridge and the domicilium in the tecnomorphs (cf. Pl. VIII, Fig. 2 and Pl. VIII, Fig. 8). It lies highest anteroventrally, and slopes moderately towards the posterior and rather steeply towards the anterior end of the dolon. The anterior boundary of the dolon is usually marked also by a rather abrupt decrease in width of the velar structure, whereas posteriorly the decrease in the width of the dolon takes place more gradually. In some species, as in *E. eutropis*, the posterior boundary of the dolon is poorly defined, and in *E. minor* both the anterior and the posterior boundary of the dolon are rather indistinct. The dimorphism in the type species of *Euprimites* is unknown at present, but as pointed out by Henningsmoen (1953a, p. 229; 1953b, p. 52) only 4 valves are known, and more abundant material will probably show the same type of dimorphism as in other species of *Euprimites*.

The subvelar field is characterized at least in most species of *Euprimites* by the presence on each valve of a distinct and rather prominent ridge. In *E. effusus* n.sp. and *E. anisus* n.sp. the left valve overlaps the right one along the free margin. On the right valve the ridge lies in the middle of the subvelar field, slightly closer to the free margin than to the velar structure, and it thus has an admarginal position. The free margin of the valve is slightly bent outwards so that in ventral view the ventral part of the subvelar field of the left valve gives the impression of possessing two ridges, a marginal and an admarginal (cf. Pl. VI, Fig. 16). Upon the left valve these species possess a rather prominent ridge adjacent to the free margin (cf. Pl. VI, Fig. 15). In closed carapaces the marginal ridge of the left valve overlaps the surface between the admarginal

ridge and the free edge of the right valve. In ventral view of a closed carapace these two ridges are rather close to each other, that of the left valve being a little broader than that of the right valve (cf. Pl. VI, Fig. 19). Also *E. locknensis* and *E. minor* possess the same arrangement of the marginal ridges. In *E. suecicus* the subvelar ridges of both valves seem to lie at the free margin, or at least very close to the margin. In this species no distinct overlap seems to be present, but in this respect the evidence is not quite clear it being very difficult to develop these thin margins undamaged. The closed carapaces of this species have, however, in ventral view on the whole the same appearance as in *E. effusus* and *E. anisus* (cf. Pl. VIII, Fig. 4).

Discussion.—In defining the genus Hessland (1949, pp. 249–250) has paid considerable attention to "the horseshoe-shaped ridge enclosing the ventral part of the sulcus". Present material has, however, shown that there exists a rather continuous morphological series from species with strongly developed horseshoe-shaped ridge to species in which there is hardly any elevation at all around the ventral part of the sulcus.

Euprimites differs distinctly from *Euprimitia*, and both genera are hardly closely related. *Euprimitia* has evidently no distinct marginal ridges, its carapace is equivalved, and subvelar field and dorsum are high (tr.). The ridge-like dolon in the heteromorphs is very different (cf. p. 277). The only clear point of similarity between these genera is found in their unisulcate condition and, to some extent, in the general shape of the sulcus.

In the present paper 7 different species of *Euprimites* are described, but the material studied contains evidence of at least 2 additional new species. As seen from the description of the generic characters the genus as defined in the present paper shows a rather high degree of variability with regard to certain characters, and it is possible that the genus may have to be split into several subgenera, once the marginal structures and the course of the contact area between the dolon and the domicilium will be better known.

Occurrence.—The type species is the earliest known species of *Euprimites*, occuring in the Lower Ordovician "*Raniceps*" limestone. The latest representatives of this genus have been recorded from 4bδ of the Oslo district, Norway. Outside Baltoscandia, except for the North German erratic boulders, no species definitely referable to *Euprimites* has so far been found.

Euprimites effusus n. sp.

Pl. VI, Figs. 10–16; Text-figs. 5B, 27A, 28, 29.

Holotype.—Left heteromorphic valve, figured on Pl. VI, Fig. 11 (SGU).

Type Locality.—Östergötland, Motala bore.

Type Stratum.—*Schroeteri* limestone (at the level of 108.20 m of the bore).

Derivation of the Name.—From Lat. *effusus* = widely distributed, referring to the wide horizontal and vertical distribution of the species.

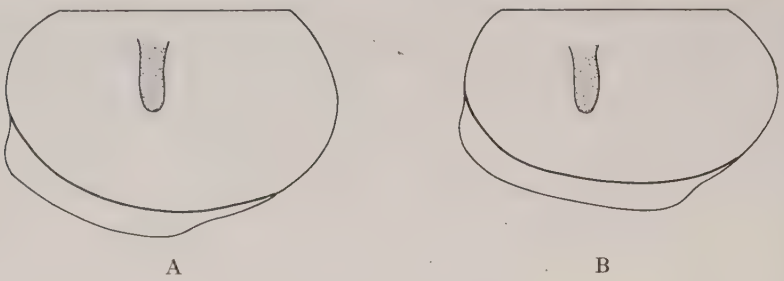


Fig. 28. *Euprimites effusus* n.sp. Diagrammatic drawings of a heteromorph with a short dolon (A) and with a long dolon (B). The contact line between the dolon and the domicilium is drawn as seen on immersion of the specimen into a liquid. A, after the specimen figured on Pl. VI, Fig. 10; B, after the holotype. × 25.

Diagnosis.—A rather large species (length of heteromorphs 1.6–1.7 mm). Sulcus relatively narrow, straight. Horseshoe-shaped ridge around the ventral part of the sulcus low, indistinct. The lateral surface of the tecnomorphs as a rule without any ornamentation; heteromorphs with a faintly reticulate anteroventral part of the domicilium.

Description.—Domicilium in ventral view rather regularly convex, highest convexity at about the mid-length of the valve or somewhat in front of it. Sulcus almost straight, comparatively narrow. The surface surrounding the ventral part of the sulcus faintly elevated, forming a low, indistinctly defined horseshoe-shaped ridge, hardly observable in younger instars. The ridge is slightly more elevated in front of the sulcus than behind it, but no distinct preadductorial node is developed. Dorsum moderately high, epicline (Pl. VI, Fig. 12).

In tecnomorphs a distinct velar ridge is present even in the earliest instar studied. Anteriorly the velar ridge becomes gradually fainter, and merges into the general anterior surface of the valve at about the mid-height of the valve. In some specimens a row of tubercles can be observed at the same level as the velar ridge almost up to the anterior cardinal corner. Posteriorly the velar structure can be followed up to the posterior cardinal corner. It becomes, however, fainter in dorsal direction, and dorsally from the middle of the posterior end of the valve is developed merely as a bend. In ventral view the velar ridge is slightly curved in lateral direction, lying highest at about the transversal line through the sulcus.

Heteromorphs with a rather broad (tr.), moderately convex, anteroventrally situated dolon. The length of the dolon varies rather considerably as is evident from the figured specimens (cf. Pl. VI, Figs. 10–11; Text-fig. 28). External surface of the dolon usually very faintly undulate. In heteromorphs the horseshoe-shaped elevation around the ventral part of the sulcus is as a rule slightly more prominent than in tecnomorphs. Anteroventrally of this elevation the

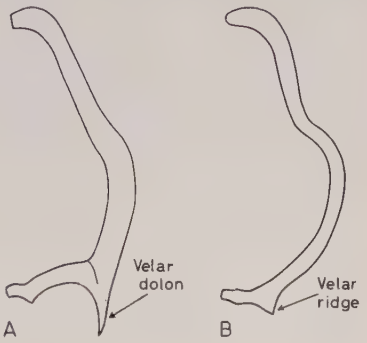


Fig. 29. *Euprimites effusus* n.sp. Diagrammatic drawings of transversal sections of a heteromorphic (A; cf. Pl. XIV, Fig. 1) and a tecnomorphic (B) valve. After thin sections. Magnification of the heteromorphic valve ×45. Note the considerable difference in the height of the tecnomorphic and heteromorphic subvelar fields.

lateral surface of the domicilium is usually faintly depressed; no conspicuous trace of such depression is observed upon tecnomorphic valves. For the subvelar field, cf. p. 302.

On the tecnomorphs no ornamentation has been observed except occasionally some small tubercles close to the anterior end of the valves. On the heteromorphs the anteroventral part of the lateral surface of well-preserved specimens as a rule faintly reticulate.

Dimensions.—See Table 16.

Discussion.—By the smooth surface of the tecnomorphs and the only anteroventrally faintly reticulated surface of the heteromorphs, by the straight, relatively narrow sulcus, and by other characters *E. effusus* clearly differs from the other known species of *Euprimites*.

Occurrence.—*E. effusus* is common in the *Platyurus* and *Schroeteri* beds in all bores and localities studied with regard to the ostracodes, except in those of Västergötland. In this province (in Norra Skagen and Stora Åsbotorp bores) the species is missing in the *Schroeteri* beds, and in beds below the *Schroeteri* mudstone specimens occur which differ in several respects from *E. effusus* of other districts. These specimens have valves with a smooth lateral surface, and the general size and appearance of *E. effusus*, but possess a more rounded outline, narrower sulcus, more conspicuous horseshoe-shaped ridge around the sulcus, and evidently also a narrower tecnomorphic velar ridge. Also the extension of the dolon seems to differ slightly from that prevailing in *E. effusus*. These specimens probably belong to a new subspecies of *E. effusus* or even to a separate new species, but for its definition better preserved material is needed. Until such material is available these specimens from Västergötland are referred to as *E.* aff. *effusus*.

Östergötland.—Motala bore (14 heterom., 80 tecnom.). *Öland.*—Böda Hamn bore (5 heterom., 39 tecnom.); Skärlöv bore (17 tecnom.); Gammalsby bore (10 heterom., 70 tecnom.); Binnerbäck (*planifrons* zone); quarry E of the northern part of lake Hornsjö (gray *Schroeteri* limestone); Seby. *Siljan district.*—Sections at Vikarbyn, Kårgärde, and Fjäcka.

Table 16.

No.	Mus. cat. no.	L. valve	H. valve	H-L	H. sulcus	Valve	Locality	Remarks
1	SGU	1.69	1.07	1.08	0.49	h—r	Motala 108.96 m	
2	,,	1.64	1.07	—	0.49	h—r	,, 108.83 m	
3	,,	1.63	1.08	1.11	0.46	h—r	,, 107.94 m	
4	,,	1.60	1.03	1.13	0.40	h—l	,, 108.20 m	Holotype: Pl. VI, Fig. 11.
5	,,	1.58	0.98	1.11	0.45	h—l	,, 106.99 m	
6	,,	1.69	1.03	1.16	—	t—l	,, 110.36 m	
7	,,	1.66	0.99	1.09	0.48	t—r	,, 107.03 m	
8	,,	1.51	0.96	—	0.48	t—r	,, 114.01 m	
9	,,	1.51	0.94	1.04	0.45	t—r	,, 108.09 m	
10	,,	1.36	0.85	0.90	0.41	t—r	,, 117.98 m	
11	,,	1.32	0.79	0.97	—	t—r	,, 107.14 m	
12	,,	1.08	0.65	0.75	0.29	t—r	,, 106.99 m	
13	UM Öl. 122	1.63	1.05	1.14	0.53	h—l	Böda Hamn 15.44 m	
14	UM Öl. 820	1.77	1.07	—	0.53	t—l	,, ,, 20.87 m	
15	UM Öl. 821	1.44	0.95	—	0.41	t—r	,, ,, 18.32 m	
16	UM Öl. 123	1.38	0.82	0.97	0.33	t—l	,, ,, 15.50 m	
17	UM Öl. 124	1.18	0.73	—	0.29	t—l	,, 20.38 m	
18	SGU	1.49	0.96	1.12	0.43	t—l	Skärlöv 4.38 m	
19	,,	1.68	1.04	1.14	0.51	h—l	Gammalsby 8.97 m	
20	,,	1.67	1.07	1.15	0.52	h—l	,, 11.78 m	
21	,,	1.69	0.96	1.12	0.53	t—r	,, 6.12 m	
22	,,	1.55	0.97	—	0.44	t—l	,, 9.16 m	
23	,,	1.50	0.97	1.01	0.49	t—l	,, 6.12 m	
24	,,	1.48	0.94	1.08	—	t—l	,, 9.40 m	
25	,,	1.36	0.82	0.97	0.38	t—l	,, 10.92 m	
26	,,	1.23	0.77	—	0.37	t—l	,, 10.92 m	
27	,,	1.20	0.76	—	0.37	t—r	,, 8.98 m	
28	,,	1.11	0.73	—	0.31	t—l	,, 6.90 m	
29	,,	1.03	0.70	—	0.30	t—l	,, 11.63 m	
30	UM Öl. 120	1.70	1.10	1.13	0.45	h—r	Öland, Seby	Figured on Pl. VI, Fig. 10.
31	UM Öl. 121	1.57	0.97	1.02	0.39	t—r	,, ,,	Figured on Pl. VI, Fig. 16.
32	UM D 425	1.52	0.92	1.09	0.41	t—l	Dal., Vikarbyn *Schroeteri a*	Figured on Pl. VI, Figs. 14–15.
33	UM D 426	1.49	0.89	1.01	0.34	t—l	Dal., Vikarbyn *Schroeteri a*	

Euprimites anisus n. sp.

Pl. VI, Figs. 17–19; Text-fig. 27B.

Holotype.—Right heteromorphic valve, UM no. Öl. 118, figured on Pl. VI, Fig. 17.

Type Locality.—Öland, Böda Hamn bore.

TYPE STRATUM.—*Platyurus* limestone (at the level of 22.40 m of the bore).

DERIVATION OF THE NAME.—From Greek ἄνισος = dissimilar.

DIAGNOSIS.—A rather large species (length of heteromorphs 1.55–1.65 mm). Sulcus moderately broad, straight, with a rather conspicuous horseshoe-shaped ridge around its ventral part. Lateral surface of the domicilium ornamented in tecnomorphs as well as in heteromorphs by a faint reticulation, and (occasionally?) a small number of scattered, minute tubercles.

DISTINGUISHING TEATURES BETWEEN *E. anisus* AND *E. effusus*.—*E. anisus* is on the whole similar to *E. effusus* and, in order to avoid repetitions in the description, only the differences between these species are indicated. The outline of *E. anisus* is generally more rounded than in *E. effusus*, being almost amplete or only slightly postplete. The sulcus somewhat longer and broader than in *E. effusus*. Ventral end of the sulcus as a rule slightly expanded. Except dorsally the sulcus is surrounded by a low, rounded, horseshoe-shaped ridge, broadest ventrally, as a rule more conspicuous in the heteromorphs than in the tecnomorphs. Heteromorphs possess, like *E. effusus*, a faint depression on the lateral surface of the domicilium anteroventrally of the horseshoe-shaped ridge. Tecnomorphic velar structure on the whole similar to that of *E. effusus*, except that anteriorly the velar ridge seems to extend slightly more in dorsal direction. In the heteromorphs the anterior end of the dolon reaches farther in dorsal direction than is usually the case in *E. effusus*, ending slightly dorsally of the mid-height of the domicilium. Owing to the rather small number of heteromorphs found the individual variability in the shape of the dolon in *E. anisus* is at present insufficiently known.

Lateral surface of the valve, except for the sulcus and the ridge around its ventral part, covered in tecnomorphs as well as in heteromorphs by a faint but distinct reticulation. Some low and rather small, scattered tubercles are occasionally observed upon the lateral surface of well-preserved specimens. Owing to the rather small number of sufficiently well-preserved specimens examined it is not quite clear whether or not these tubercles are a constant feature of the ornamentation of this species.

DIMENSIONS.—See Table 17.

Table 17.

No.	Mus. cat. no.	L. valve	H. valve	H-L	H. sulcus	Valve	Locality	Remarks
1	UM Öl. 117	1.64	1.04	1.06	0.48	h—r	Böda Hamn 22.30 m	
2	UM Öl. 118	1.57	1.01	1.06	0.47	h—r	Böda Hamn 22.40 m	Holotype Pl. VI, Fig. 17.
3	UM Öl. 119	—	0.82	—	0.40	t—r	Böda Hamn 22.65 m	Figured on Pl.VI, Fig. 18.

Discussion.—*Euprimites anisus* occurs in the *Platyurus* limestone together with *E. effusus* with which it agrees in size and the general outline. In the *Platyurus* limestone corroded specimens of *Euprimites* of this general type are, therefore, hardly determinable specifically. Well-preserved specimens differ, however, rather distinctly. *Euprimites bursellus* shares with *E. anisus* the type of ornamentation, but the heteromorphs of the former species are much smaller, their outline more oblong, and their sulcus of rather different shape. It occurs, moreover, at a higher stratigraphic horizon.

Occurrence.—*E. anisus* n.sp. is a rare species, and has been found only in the *Platyurus* beds.

Öland.—Böda Hamn bore (2 heterom., 2 tecnom.); Gammalsby bore (4 tecnom.). *Östergötland.*—Motala bore (2 heterom., 1 tecnom.). *Siljan district.*—Fjäcka, 70–100 cm above the lower boundary of the *Platyurus* limestone (2 heterom., 2 tecnom.).

Euprimites locknensis (Thorslund, 1940)

Pl. VII, Figs. 1–7; Text-fig. 27D.

1940 *Euprimitia ? locknensis* n.sp.—Thorslund, p. 165, Pl. 4, Fig. 7.
1948 Euprimitia cf. *locknensis* Thorsl.—Thorslund, pp. 349–350.
1948 Euprimitia locknensis Thorsl.—Thorslund, p. 347.
1949 Euprimites locknensis (Thorslund)—Hessland, p. 250.

Holotype.—Right heteromorphic valve, figured by Thorslund 1940, Pl. 4, Fig. 7 (SGU).

Type Locality.—Exposure 1.2 km W of the railway station of Tandsbyn, Brunflo-Lockne area, Jämtland.

Type Stratum.—*Ludibundus* limestone.

Diagnosis.—A species of moderate size (length of the heteromorphs 1.35–1.55 mm). Sulcus rather broad and long, more or less straight, ventral part distinctly expanded and surrounded by a conspicuous, rounded ridge. Ornamentation consisting of a distinct reticulation.

Description.—Outline nearly amplete, posterior end more rounded. Highest convexity somewhat behind the sulcus. Dorsum low, epicline. Sulcus rather long and broad in comparison with the other described species of *Euprimites*, almost straight, slightly constricted at the middle, ventral part distinctly expanded and surrounded by a distinct rounded, horseshoe-like ridge. The latter is highest ventrally, very low or hardly developed behind the sulcus, better defined in front of it, reaching dorsally to the constriction of the sulcus, and ending there in a faint expansion which forms an indistinct preadductorial node. Anteroventrally of the ridge the lateral surface of the domicilium is distinctly depressed, the depression being conspicuous even in late instars of the tecnomorphs, but very faint or missing in younger instars; it is as a rule deeper and distincter in heteromorphs than in tecnomorphs.

Table 18.

No.	Mus. cat. no.	L. valve	H. valve	H-L	H. sulcus	Valve	Locality	Remarks
1	SGU	1.52	0.86	1.15	0.44	h—l	1.2 km W of Tandsbyn railway station	
2	,,	1.46	0.83	1.04	0.43	h—r	,,	Holotype, THORSLUND, 1940, Pl. 4, Fig. 7.
3	,,	1.40	0.75	~0.87	0.40	h—r	,,	
4	,,	1.38	0.76	0.87	0.41	h—r	,,	
5	,,	1.28	0.73	—	0.34	t—r	,,	Figured on Pl. VII, Figs. 4–5.
6	,,	1.40	0.81	—	0.40	h—r	Hallen, kongl.	
7	RM Ar. 20125	1.44	0.88	0.99	0.41	h—r	Böda Hamn	Figured on Pl. VII, Fig. 2.
8	RM Ar. 20129	1.26	0.72	0.94	0.31	t—l	,, ,,	Figured on Pl. VII, Figs. 6–7.
9	UM Öl. 116	1.36	0.76	0.87	0.37	h—r	,, ,, 1.70 m	Figured on Pl. VII, Fig. 3.
10	SGU	1.30	0.83	—	0.41	h—r	Smedsby Gård 97.15 m	
11	,,	1.44	0.81	1.03	0.46	t—l	,, ,, 99.23 m	
12	,,	1.34	0.81	—	0.47	h—r	Norra Skagen 10.45 m	
13	,,	1.40	0.76	1.02	0.42	t—l	,, ,, 10.47 m	
14	UM Vg. 702	1.35	0.81	1.04	—	h—l	Kullatorp 88.37 m	
15	UM Vg. 703	1.16	0.68	—	0.39	t—r	,, 87.36 m	
16	UM Vg. 704	1.14	0.70	—	0.35	t—l	,, 88.37 m	

Tecnomorphs with a narrow velar ridge even in the youngest instars studied. In ventral view the velar ridge is conspicuously curved in lateral direction, lying highest at about the transversal line through the sulcus (cf. Pl. VII, Figs. 5, 7). In this respect *E. locknensis* resembles *E. bursellus* which also possesses a strongly laterally curved tecnomorphic velar ridge. The velar ridge is distinct anteriorly almost up to the anterior cardinal corner, becoming rather faint at its dorsal end, and disappearing near the dorsal margin. In posterior direction it can be followed almost up to the posterior cardinal corner. In lateral view the ventral margin of the velar ridge tends usually to be more or less straight in the middle, more or less parallel to the dorsal margin of the valve.

Heteromorphs with a rather broad and long dolon, its ventral margin being more or less straight and nearly parallel to the dorsal margin of the valve. Inner part of the dolon more or less plane, peripheral part slightly convex. Posteriorly the dolon begins to decrease in width somewhat behind the mid-length of the postadductorial area, and changes into a velar ridge at about the

point where the velar structure reaches the posterior end of the valve. Anteriorly the dolon can be followed up to the height of the middle of the sulcus. The contact area between the dolon and the domicilium is placed more laterally than the velar ridge in the tecnomorphs, lying highest anteroventrally.

The lateral surface of the domicilium, except that of the sulcus and the ridge around it, is ornamented with a distinct reticulation, and usually also with an irregular row of tubercles near the dorsal margin of the valve.

Subvelar field of both valves with a strong ridge. Upon the right valve the ridge has an admarginal position, lying at some distance from the free edge (cf. Pl. VII, Fig. 5). The admarginal ridge is, however, placed closer to the free edge than in *E. effusus* and *E. anisus*. On the left valve the ridge seems to lie at the free edge (cf. Pl. VII, Fig. 7). Actual closure of the carapace along the free margin not observed.

Dimensions.—See Table 18.

Discussion.—*Euprimites locknensis* differs distinctly from other known species of *Euprimites*, particularly by the distinct reticulation of the lateral surface, the fairly long and broad sulcus with expanded ventral part, and the more or less straight ventral margin of the long dolon. From the somewhat similar *E. minor* *E. locknensis* differs by its much larger size, different shape of the dolon, shape of the sulcus, and other characters.

Occurrence.—*Euprimites locknensis* is one of the most common ostracodes in the *Ludibundus* formation and evidently confined to these beds. It has been found throughout the whole vertical extension of these beds.

Autochthonous of Jämtland.—Exposure 1.2 km W of the railway station of Tandsbyn; Öd; Hallen. *Siljan district.*—Fjäcka. *Östergötland.*—Smedsby Gård bore (9 heterom., 30 tecnom.). *Öland.*—Böda Hamn bore (7 heterom., 30 tecnom.); exposure at the beach of Böda Hamn. *Västergötland.*—Norra Skagen bore (12 heterom., 26 tecnom.); Kullatorp bore (12 heterom., 24 tecnom.); Stora Åsbotorp bore (7 heterom., 20 tecnom.).

Euprimites bursellus n. sp.

Pl. VII, Figs. 16–20; Text-fig. 27E.

Holotype.—Left heteromorphic valve, UM no. Öl. 113, figured on Pl. VII, Fig. 16.

Type Locality.—Öland, Böda Hamn bore.

Type Stratum.—Lowermost *Crassicauda* limestone (at the level of 12.02 m of the bore).

Derivation of the Name.—Diminutive from Lat. *bursa*, sack.

Diagnosis.—A rather small species (length of heteromorphs 1.1–1.3 mm). Sulcus moderately broad, ventral part distinctly curved anteroventrally, scarcely expanded. Ridge around the ventral part of the sulcus low, poorly defined. Dolon considerably expanded anteroventrally, gradually decreasing

in width (tr.) in posterior direction, and changing into a velar ridge without any distinct boundary. Surface with a faint reticulation.

Description.—Outline of the tecnomorphic valves nearly amplete. Highest convexity behind the sulcus at about the middle of the valve. Dorsum low, rather plane, almost orthocline. Sulcus moderately broad, very slightly constricted in the middle, ventral part curved anteroventrally, hardly expanded, having about the same width (long.) as the dorsal part. Surface of the valve around the sulcus, except dorsally, slightly elevated, forming an indistinct ridge. In front of the sulcus the dorsal end of the ridge expands slightly, forming a low, anteriorly poorly defined preadductorial node, which causes the slight constriction of the sulcus.

Tecnomorphs with a distinct velar ridge even in the youngest instars studied. Anteriorly the velar structure can be traced almost up to the anterior cardinal corner. At the anterior end of the valve it has the shape of a rounded indistinct ridge, resembling a bend in its dorsal part. Posteriorly the velar structure seems to coalesce with the strong marginal ridge already before reaching the posterior end of the valve. The ridge then continues up to the posterior cardinal corner, being separated from the domicilium by a shallow, but usually rather distinct furrow. In ventral view the velar ridge is slightly arched upwards, lying highest somewhat in front of the transversal line through the ventral end of the sulcus (cf. Pl. VII, Fig. 20). In the heteromorphs the dolon expands considerably in anteroventral direction, and in specimens with undamaged velum the dolon projects as a rule in anterior direction considerably beyond the anterior end of the domicilium. The anterodorsal end of the dolon reaches up to the height of the middle of the sulcus or slightly more dorsally. In posterior direction the dolon decreases gradually in width, and merges smoothly into a velar ridge of the tecnomorphic type at about the mid-length of the postadductorial area. In heteromorphs the surface of the domicilium is as a rule slightly depressed anteroventrally of the horseshoe-shaped ridge. In tecnomorphs occasionally only a faint trace of this depression can be observed in the adult stage and in late instars. Subvelar field of both valves with a distinct ridge. It could, however, not be clearly observed whether the ridge of the right valve has an admarginal position or not.

The lateral surface of the valve, excepting the sulcus and the ridge around it, is ornamented by a faint reticulation and usually also by a row of minute tubercles close to the dorsal margin of the valve. On the surface of even slightly corroded valves the reticulation is scarcely visible.

Dimensions.—See Table 19.

Discussion.—It is possible that *E. bursellus* may in future prove be identical with *Primitia bursa* Krause. The latter species has been referred by Bassler & Kellett (1934, p. 314) to *Eurychilina*, and by E. A. Schmidt (1941, pp. 27–29) to *Craspedobolbina*, but is undoubtedly a species of *Euprimites* as pointed out already by Hessland (1949, p. 250). *Euprimites bursa* as illustrated by

Table 19.

No.	Mus. cat. no.	L. valve	H. valve	H-L	H. sulcus	Valve	Locality	Remarks
1	UM Öl. 113	1.14	0.69	0.84	0.37	h—l	Böda Hamn 12.02 m	Holotype. Pl. VII, Fig. 16.
2	UM Öl. 114	1.12	0.67	0.85	0.34	t—l	,, ,, 13.05 m	Figured on Pl. VII, Figs. 19–20.
3	SGU	1.10	0.70	—	0.40	h—r	Gammalsby 8.65 m	
4	,,	1.15	0.67	—	0.39	t—r	,, 8.20 m	
5	,,	1.03	0.60	0.76	0.32	t—r	,, 5.75 m	
6	UM Öl. 115	1.20	0.73	0.82	0.36	h—r	Öland, Seby	
7	SGU	1.27	0.69	0.88	0.36	h—r	Motala 100.99 m	
8	,,	1.15	0.70	0.65	0.35	h—l	,, 100.05 m	Figured on Pl. VII, Fig. 18.
9	,,	1.12	0.67	—	0.35	h—r	,, 101.42 m	
10	,,	0.99	0.59	—	0.31	t—l	,, 101.60 m	
11	,,	1.13	0.72	0.87	0.38	h—r	Stora Åsbotorp 74.37 m	Figured on Pl. VII, Fig. 17.
12	,,	1.13	0.68	—	0.37	h—r	Stora Åsbytorp 68.95 m	

Krause (1889, Pl. I, Figs. 7 and 8) has a moderately broad sulcus, slightly constricted at about its middle, and an anterolaterally curved ventral part of the sulcus. Moreover, the heteromorphic valve figured on Pl. I, Fig. 8 by Krause (1889) is of about the same general size (length 1 mm according to Krause 1889, p. 9, but probably slightly longer as the foremost part of the dolon seems to be broken off) than that of *E. bursellus* and considerably smaller than the other more or less contemporaneous species of *Euprimites*. Yet *E. bursa* is stated by Krause (1889, p. 9) to be without ornamentation, and as *E. bursellus* has a reticulate ornamentation these species may be different. On this account, *E. bursellus* has been regarded in the present paper as a separate species.

The shape of the sulcus and that of the dolon of *E. bursellus* are rather distinctive, and these characters together with the ornamentation and other features distinguish *E. bursellus* clearly from the other known species of *Euprimites*.

Occurrence.—*Euprimites bursellus* appears already in the *Schroeteri* beds, being more abundant in their upper part, and continues through the *Crassicauda* beds.

Öland.—Böda Hamn bore (2 heterom., 7 tecnom.); Gammalsby bore (3 heterom., 7 tecnom.); quarry SW of Källa church; Seby. *Siljan district.*—Sections at Vikarbyn and Kårgärde. *Östergötland.*—Motala bore (12 heterom., 15 tecnom.); Smedsby Gård bore (1 tecnom.). *Västergötland.*—Kullatorp bore (1 tecnom.); Stora Åsbotorp bore (4 heterom., 3 tecnom.).

Euprimites cf. *eutropis* (Öpik, 1937)

Pl. VII, Figs. 8–11.

A small number of tuberculate specimens of *Euprimites* from the *Crassicauda* limestone resemble on the whole *E. eutropis* (Öpik), but differ in some minor details, especially in the shape of dolon. In at least some of the species of *Euprimites*, the length (long.) of the dolon varies rather considerably (cf. *E. effusus* and *E. suecicus*), and as the material of the species under description is rather small, it is difficult at present to ascertain the degree of individual variation of its characters. Also in the Estonian material of *E. eutropis* the individual variation is still unknown, and the present writer had at his disposal no topotype material of this species for comparison.

Description.—Outline almost amplete. The domicilium is rather weakly and more or less uniformly convex. Highest convexity posteroventrally of the ventral end of the sulcus. Sulcus of moderate width and length (tr.), usually slightly constricted in the middle, and with faintly expanded ventral part. A low, rounded, as a rule feebly developed ridge surrounds the sulcus except dorsally and behind, being usually most distinct anteroventrally. A preadductorial node is scarcely distinguishable. Dorsum low, faintly convex, almost orthocline. A distinct, rather large, smooth node on the anterior corner field present in almost all specimens studied.

Tecnomorphs from the erratic boulder Bergsbrunna no. 1 with a distinct, rather broad, in lateral view slightly concave velar ridge, expanding anteroventrally. Posteriorly the velar structure can be followed up to the posterior cardinal corner, being shaped at the anterior end of the valve as a rounded ridge, and delimited from the lateral surface of the domicilium by a fairly distinct furrow. Anteriorly the velar structure seems to become confluent with the marginal ridge slightly before reaching the anterior end of the valve, but the actual fusion could not be observed on account of the difficulties in exposing the subvelar field. In ventral view the velar ridge runs in a laterally directed curve, the subvelar field being highest anteroventrally. The tecnomorphic velar structure of valves from other localities could not be examined in detail, the tecnomorphs found being either fragmentary or badly preserved.

In the heteromorphs the dolon shows a rather high degree of variation. In the specimens from the boulder Bergsbrunna no. 1 the dolon is by an abrupt change in convexity and width distinctly delimited anteriorly and posteriorly. It is moderately convex and, except for the ends, of a more or less uniform width throughout its extension. The contact area between the dolon and the domicilium is placed relatively high laterally, curving rather abruptly down at both ends to the level of the tecnomorphic type of the velar structure. Posteriorly the dolon changes rather abruptly into a comparatively broad and distinctly concave velar ridge in front of the mid-length of the postadductorial area.

Anteriorly the dorsal end of the dolon lies slightly dorsally of the longitudinal line through the ventral end of the sulcus.

In the heteromorphs from other localities the dolon is rather long, and faintly convex. The contact line between the dolon and the domicilium is on the whole as in the specimens from Bergsbrunna no. 1. At its posterior end the dolon decreases rather abruptly in width, and changes into a narrow velar ridge, which becomes obsolete before reaching the posterior end of the valve. In this respect these specimens seem to differ from the two from Bergsbrunna no. 1 and from *E. eutropis*. In heteromorphs from Bergsbrunna no. 1 the velar ridge behind the dolon is rather broad, and distinctly concave in both of the heteromorphic valves examined, and the velar structure reaches somewhat higher up dorsally. In *E. eutropis* the dolon decreases gradually in width in posterior direction, and the posterior boundary of the dolon seems to be rather poorly defined, if we may judge from the figures by Öpik (1937).

The lateral surface of the domicilium, except for the sulcus, the ridge surrounding the ventral end of the sulcus, and the node on the anterior corner field, ornamented with scattered, moderately large tubercles, arranged in irregular rows close to the dorsal margin. In the specimens from the erratic boulder no. 10 of Erken a faint reticulation is visible between the tubercles (cf. Pl. VII, Fig. 9). In the other specimens no such reticulation has been observed.

Dimensions.—See Table 20.

Table 20.

No.	Mus. cat. no.	L. valve	H. valve	H-L	H. sulcus	Valve	Locality	Remarks
1	UM B 231	1.33	0.73	1.06	0.31	h—c	Bergsbrunna, boulder nr. 1	Figured on Pl. VII, Fig. 10.
2	UM B 232	1.33	0.78	—	0.42	h—l	,,	
3	UM B 233	1.28	0.69	0.99	0.30	t—r	,,	Figured on Pl. VII, Fig. 11.
4	UM B 234	1.23	0.74	0.93	0.34	h—r	Erken, boulder no. 10	Figured on Pl. VII, Fig. 9.
5	UM Öl. 125	1.31	0.75	0.95	0.32	h—r	Böda Hamn, 10.60 m	
6	SGU	1.20	0.72	0.90	0.30	h—r	Smedsby Gård 119.40 m	Figured on Pl. VII, Fig. 8.

Discussion.—The specimens determined here as *E.* cf. *eutropis* seem to be rather close to *E. eutropis* Öpik, and it is not excluded that more material may show them to be conspecific, or that the differences are of merely subspecific value. With regard to the rather considerable variability of the material described above, it is, on the other hand, not entirely excluded that a larger

material may prove the existence in the *Crassicauda* beds of Sweden of several different tuberculate species of *Euprimites*.

The specimens from the *Ludibundus* limestone of the Brunflo-Lockne area, Jämtland, determined by THORSLUND (1940, pp. 25, 186) as *Euprimitia*? *eutropis* ÖPIK evidently belong to a new species of *Euprimites*. It differs from *E. eutropis* and from *E.* cf. *eutropis* particularly by a relatively very short dolon the anterior end of which is placed high dorsolaterally.

The specimens of *E. eutropis* figured by ÖPIK (1937) all belong to the heteromorphic type. HENNINGSMOEN (1953b, p. 52) pointed out that *Haploprimitia inconstans* ÖPIK, 1937, is probably based on larval (tecnomorphic) instars of *E. eutropis*. This seems to be a likely assumption.

OCCURRENCE.—The species determined here as *E.* cf. *eutropis* has been found in the *Crassicauda* limestone.

South Bothnian area.—Erratic boulders Erken no. 10 (3 heterom., 2 tecnom.) and Bergsbrunna no. 1 (2 heterom., 1 tecnom.). *Öland.*—Böda Hamn bore (2 heterom.). *Östergötland.*—Smedsby Gård bore (1 heterom., 1 tecnom.). *Västergötland.*—Norra Skagen bore (2 tecnom.); Stora Åsbotorp bore (2 tecnom.).

Euprimites minor (THORSLUND, 1940)

Pl. VII, Figs. 12–15.

1940 *Euprimitia minor* n.sp.—THORSLUND, pp. 164–165, Pl. I, Figs. 11–12.
1949 Euprimites minor (THORSLUND)—HESSLAND, p. 250.
1953b Euprimites ? suecica (THORSLUND)—HENNINGSMOEN, p. 51.

HOLOTYPE.—Right tecnomorphic valve, UM no. T9, figured by THORSLUND 1940, Pl. I, Figs. 11–12.

TYPE AREA.—Södermanland, Tvären area, Ringsö, erratic boulders.

TYPE STRATUM.—Lowermost *Ludibundus* limestone.

DIAGNOSIS.—A small species (length of heteromorphs 0.90–1.05 mm). Sulcus moderately broad, comparatively short, nearly straight, slightly constricted in the middle, ventral part somewhat expanded, the width (long.) of the expanded part not exceeding the width of the dorsal part. Dolon relatively narrow (tr.) and long, more or less plane. Surface ornamented with a distinct reticulation and a small number of minute tubercles.

MATERIAL.—16 tecnomorphic valves, 3 tecnomorphic carapaces, and 4 heteromorphic valves.

DESCRIPTION.—Outline nearly amplete. The domicilium is moderately and rather regularly convex; greatest convexity sometimes in front of, and sometimes behind the sulcus. Dorsum low, plane, nearly orthocline. Sulcus moderately broad, rather short (tr.), faintly but distinctly constricted in the middle, with an inconspicuously expanded ventral part. The width (long.) of the expanded part does not exceed the width of the dorsal part of the sulcus, and seems usually to be even a little less. Ventral end of the sulcus rounded, sur-

rounded by a low elevation, the dorsal end of which is slightly expanded and swollen in front of the sulcus, forming a flattened preadductorial node.

Tecnomorphs with a distinct velar ridge also in the youngest instars examined. Anteriorly the velar ridge becomes obsolete before reaching the longitudinal line through the middle of the sulcus, the continuation of the velar structure in dorsal direction being usually marked by a row of tubercles. Posteriorly the extension of the velar structure is about the same as anteriorly. In ventral view the velar ridge follows a gentle, laterally directed curve, the highest point of which lies usually at about the transversal line through the sulcus (cf. Pl. VII, Fig. 13).

In heteromorphs the velar structure is developed ventrally and anteroventrally as a rather narrow flange, more or less plane ventrally, and concave near its anterodorsal end. The lateral surface of the dolon is as a rule faintly undulate. The contact area between the dolon and the domicilium seems on the whole to agree with that between the corresponding part of the tecnomorphic velar ridge and the domicilium. In the heteromorphs the anteroventral part of the area is perhaps situated slightly higher upon the side. Anteroventrally of the sulcus no apparent depression could be observed in the lateral surface of the domicilium.

Subvelar field of both valves with a distinct, rather strong ridge. The ridge of the right valve occupies an admarginal, that of the left valve a marginal position. In closed carapaces the left valve evidently slightly overlaps the right valve along the free margin.

The ornamentation of the lateral surface of the valve, except for the sulcus and the ridge around it, consists of a distinct reticulation with a small number of scattered minute tubercles. The tubercles are more numerous near the dorsal margin, forming there two irregular rows. The area dorsally of the longitudinal line through the dorsal end of the sulcus seems to be almost devoid of pits.

Dimensions.—See Table 21.

Discussion.—*Euprimites minor* resembles on the whole the type species, *E. reticulogranulatus*, of which the largest specimen known (holotype) is only slightly larger than that of *E. minor*. *Euprimites reticulogranulatus* also has the same general type of ornamentation. In this species the sulcus, however, exhibits a different shape, being strongly expanded ventrally, and surrounded by a much higher and stronger ridge.

Euprimites minor was believed by Henningsmoen (1953b, p. 57; cf. also 1953a, p. 230) to be founded upon young instars of *E. suecica*. This, however, is certainly not the case. The specimens of *E. suecica* of the same size as *E. minor* have no velar ridge, a different outline, and a narrow, straight sulcus. Furthermore, the ornamentation is quite different.

Occurrence.—*Euprimites minor* has been found only in the boulders of the lowermost *Ludibundus* limestone at Tvären, Södermanland.

Table 21.

No.	UM Mus. cat. no.	L. valve	H. valve	H-L	H. sulcus	Valve	Remarks
1	T 96	1.05	0.62	0.83	0.27	h—l	Figured on Pl. VII, Fig. 15.
2	T 97	1.01	0.59	0.83	0.23	h—l	Figured on Pl. VII, Fig. 14.
3	T 100	1.00	0.62	0.77	0.27	h—r	
4	T 99	0.94	0.56	—	0.31	h—r	
5	T 98	1.02	0.60	0.82	0.25	t—l	Figured on Pl. VII, Figs. 12–13.
6	T 101	0.93	0.57	0.73	0.23	t—r	
7	T 102	0.92	0.54	0.72	0.23	t—l	
8	T 103	0.91	0.57	0.70	0.25	t—r	
9	T 104	0.87	0.53	0.67	0.23	t—r	
10	T 9	0.85	0.52	—	0.19	t—r	Holotype. THORSLUND 1940, Pl. 1, Figs. 11–12.
11	T 105	0.78	0.49	0.62	0.19	t—r	
12	T 106	0.77	0.47	0.64	0.17	t—c	

Euprimites suecicus (THORSLUND, 1940)

Pl. VII, Fig. 21; Pl. VIII, Figs. 1–11; Text-figs. 7, 27C, 30, 31.

1940 *Ctenobolbina suecica* n.sp.—THORSLUND, pp. 172–173, Pl. 2, Figs. 13, 14, Pl. 3, Fig. 14.

1953a *Euprimites suecica* (THORSLUND)—HENNINGSMOEN, pp. 229–230.

non 1953b *Euprimites ? suecica* (THORSLUND)—HENNINGSMOEN, Pl. 1, Fig. 16, Pl. 5, Fig. 2 (= *Euprimites* n.sp.).

HOLOTYPE.—Left heteromorphic valve, figured on Pl. VII, Fig. 21; THORSLUND 1940, Pl. 2, Fig. 14 (SGU).

TYPE LOCALITY.—Exposure 1.2 km W of the railway station of Tandsby, Brunflo-Lockne area, Jämtland.

TYPE STRATUM.—Lower *Ludibundus* limestone.

DIAGNOSIS.—A rather large species (length of heteromorphs 1.15–1.75 mm). Sulcus narrow, straight, ventral part only inconspicuously expanded, almost without any surrounding elevation. Outline strongly preplete. No velar ridge in instars shorter than 1.2 mm. Lateral surface of well-preserved valves with a very faint reticulation, rest of surface covered with scattered rather small tubercles of somewhat varying size.

MATERIAL.—A rather large number of specimens.

DESCRIPTION.—Outline distinctly postplete. Domicilium in ventral view rather regularly convex, highest convexity slightly behind the sulcus. Sulcus practically straight, transversally directed, narrow, ventral part very slightly expanded and surrounded by a low, often scarcely discernible elevation. In large specimens the dorsal end of the latter is slightly expanded in front of the sulcus so as to form a flattened preadductorial node. Dorsum low, epicline (Pl. VIII, Fig. 3).

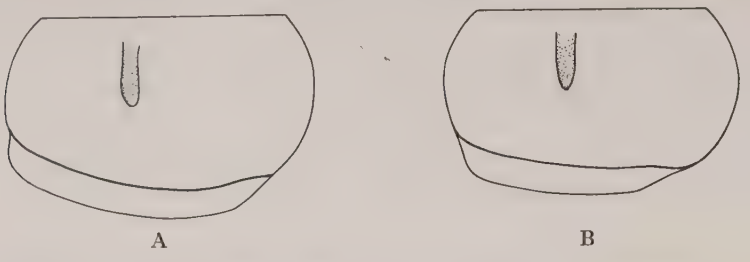


Fig. 30. *Euprimites suecicus* (THORSL.). Diagrammatic drawings of a heteromorph with a long dolon (A) and with a short dolon (B). The contact line between the dolon and the domicilium is drawn as seen on immersion of the specimen into a liquid. A, after the specimen figured on Pl. VIII, Fig. 6; B, after that on Pl. VIII, Fig. 9. × 25.

Large tecnomorphs with a distinct velar ridge, no such structure being present in young instars. There is some overlap in size between the specimens with a distinct velar ridge, and those without a velar structure. The latter may be developed on specimens with a length of 1.25 mm and more, but specimens without a velar structure have been observed up to a length of 1.35 mm (cf. Fig. 7). Ventrally and anteroventrally large specimens possess a prominent, rounded velar ridge. Farther dorsally the ridge gradually changes into an indistinct bend, often carrying a row of tubercles. The change from a ridge into a bend occurs anteriorly at about the middle of the anterior end of the valve, whereas posteriorly the velar structure can usually be followed slightly higher up in dorsal direction. In ventral view the velar structure is slightly arched in lateral direction, lying highest anteroventrally (cf. Pl. VIII, Fig. 2). In young instars the velar structure is bend-like or missing (cf. Pl. VIII, Fig. 11). Subvelar field comparatively very low (cf. Pl. VIII, Figs. 2, 4).

In heteromorphs the anteroventral part of the velar structure is strongly expanded, forming a rather broad (tr.) dolon, and the contact area between the dolon and the domicilium is placed considerably higher upon the side of the domicilium than the corresponding part of the velar structure in the tecnomorphs (cf. Pl. VIII, Fig. 8). The ends of the dolon are distinctly marked by a rather abrupt decrease in the width of the velar structure, and by an equally abrupt curve of the contact area. The length of the dolon varies rather considerably (cf. Fig. 30), and there is evidently no correlation between it and the size of the valve (cf. Fig. 7). The variation in the extension of the dolon is indeed so great that the present writer originally supposed the material from Tvären to consist of several different species. A close study of numerous specimens has, however, displayed no evident differences in other characters between the valves with long and short dolon. The differences in the length of the dolon thus seem to be due to individual variation of about the same magnitude as in *E. effusus*.

Large specimens of both valves have a distinct marginal ridge at the free margin, that of the left valve being obviously slightly more prominent (Pl.

Fig. 31. *Euprimites suecicus* (THORSL.). Diagrammatic drawing of a transversal section of a heteromorphic valve. × 50.

VIII, Fig. 4). As far as can be judged from the material studied no conspicuous overlap does seem to occur along the free margin. In young instars no marginal ridges are developed (Pl. VIII, Fig. 11). These ridges seem to appear more or less simultaneously with the velar ridge.

The ornamentation consists of small scattered tubercles of somewhat varying size. They are usually more closely placed near the dorsal margin, forming one or two irregular rows. The surface of well preserved specimens shows a faint reticulation. On some specimens it appears as if the reticulation might also be called a reticulo-granulation, since it is formed by minute granules arranged in rows so as to produce a reticulate appearance.

DIMENSIONS.—See Table 22.

In the table, the following terms have been used to denote differences in the development of the velar structure: "short" = comparatively short (long.) dolon; "long" = comparatively long dolon; "interm." = dolon of an intermediate longitudinal length; "ridge" = velar structure developed as a ridge; "bend" = velar structure faint, bend-like; "missing" = no distinct velar structure developed. The holotype (specimen no. 1) has been found in an exposure 1.2 km W of the Tandsbyn railway station, the other measured specimens in erratic boulders of Tvären area, Södermanland.

DISCUSSION.—By its distinctly postplete outline, straight, narrow, and relatively shallow sulcus, comparatively feebly developed velar ridge, its ornamentation, and other characters *E. suecicus* clearly differs from other known species of *Euprimites*. There occur, however, in the *Crassicauda* limestone one or two still undescribed new species of *Euprimites* which resemble *E. suecicus*, but differ in the shape of the dolon.

The specimens from 4bδ of the Oslo area described by HENNINGSMOEN (1953b) as *E.? suecica* belong, in the light of the specimens studied by the present writer, to a new species of *Euprimites* close to *E. locknensis*.

OCCURRENCE.—*Euprimites suecicus* has been found only in the *Ludibundus* limestone.

Jämtland, Brunflo-Lockne area. Exposure 1.2 km W of the railway station of Tandsbyn. *Södermanland*, Tvären area. Ringsö (boulders).

Table 22.

No.	Mus. cat. no.	L. valve	H. valve	H-L	H. sulcus	Valve	Velar structure	Remarks
1	SGU	1.73	1.10	1.31	0.48	h—l	short	Holotype. Pl. VII, Fig. 21; Thorslund 1940, Pl. 2, Fig. 14.
2	UM T 107	1.67	—	1.28	0.46	h—l	interm.	Figured on Pl. VIII, Figs. 7–8.
3	UM T 108	1.57	1.00	—	0.44	h—l	long	,, ,, Pl. VIII, Fig. 6.
4	UM T 32a	1.56	1.02	—	0.42	h—r	long	Thorslund, 1940, Pl. 3, Fig. 4.
5	UM T 110a	1.52	1.00	1.11	0.44	h—r	long	Figured on Pl. VIII, Fig. 5.
6	UM T 111	1.51	0.94	1.13	0.38	h—l	short	,, ,, Pl. VIII, Fig. 9.
7	UM T 112	1.45	0.92	1.12	0.38	h—l	interm.	
8	UM T 113	1.39	0.89	1.11	0.36	h—l	long	
9	UM T 114a	1.24	0.77	0.98	—	h—l	long	
10	UM T 115a	1.17	0.72	—	0.31	h—r	short	
11	UM T 116	1.85	1.09	1.38	0.50	t—c	ridge	Figured on Pl. VIII, Figs. 3–4.
12	UM T 117	1.57	0.87	1.16	0.37	t—r	,,	
13	UM T 118	1.55	0.93	1.08	0.39	t—r	,,	Figured on Pl. VIII, Figs. 1–2.
14	UM T 32b	1.53	0.93	1.11	0.39	t—r	,,	
15	UM T 120	1.48	0.94	1.13	0.38	t—r	,,	
16	UM T 121	1.48	0.85	1.07	0.38	t—l	,,	
17	UM T 110b	1.36	0.79	1.03	0.43	t—r	,,	
18	UM T 122	1.35	0.82	1.05	0.32	t—l	"bend"	
19	UM T 126	1.30	0.75	0.96	0.34	t—l	missing	Figured on Pl. VIII, Figs. 10–11.
20	UM T 124	1.34	0.82	1.04	0.33	t—l	,,	
21	UM T 114b	1.30	0.79	0.99	—	t—r	ridge	
22	SGU	1.29	0.78	0.96	0.34	t—r	,,	
23	UM T 125	1.26	0.75	0.95	0.31	t—l	missing	
24	UM T 94b	1.23	0.70	0.94	0.25	t—l	,,	
25	UM T 127	1.18	0.65	0.90	0.29	t—r	,,	
26	UM T 20	1.17	0.70	0.84	—	t—c	,,	Thorslund 1940, Pl. 2, Fig. 13.
27	UM T 129	1.10	0.66	0.82	0.25	t—l	,,	
28	UM T 123	1.35	0.82	1.04	0.38	t—c	"bend"	
29	UM T 130	1.02	0.60	—	0.25	t—l	missing	
30	UM T 131	0.96	0.59	0.70	0.24	t—r	,,	
31	UM T 132	0.90	0.56	0.68	0.23	t—r	,,	
32	UM T 133	0.70	0.38	0.55	~0.15	t—r	,,	

Gen. *Levisulculus* n.gen.

Type Species.—*Levisulculus lineatus* n.sp.

Diagnosis.—Almost non-sulcate, with an indistinct, as a rule slightly curved, narrow sulcal depression, mostly with a small preadductorial node in front of it. Outline usually rather strongly preplete. Tecnomorphs with a moderately broad to narrow velar flange, not reaching the posterior cardinal corner. Heteromorphs with a distinct, rather strongly convex dolon which is usually

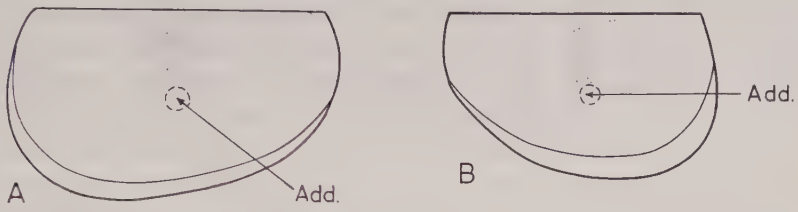


Fig. 32. Diagrammatic drawings of tecnomorphic valves to show the position of the scar of the adductor muscle (*Add*). A, *Levisulculus troedssoni* (THORSL.) after the specimen figured on Pl. VIII, Fig. 16. B, *Levisulculus granulosus* (THORSL.) after the holotype. × 30.

broadest anteriorly. A small, rounded muscle scar is situated at about the mid-height of the lateral surface of the valve or slightly ventrally of it.

SPECIES.—*Levisulculus lineatus* n.sp.
Primitia? extraria ÖPIK, 1937
Primitia troedssoni THORSLUND, 1940
Primitia granulosa THORSLUND, 1940.

GENERIC CHARACTERS.—In all species referred here to *Levisulculus* the outline is rather strongly preplete. Hinge-line long, only slightly shorter than the length of the domicilium. Dorsum low to moderately high (tr.), almost orthocline to slightly epicline. Preadductorial node usually low, indistinctly defined anteriorly. Behind it the surface of the valve is slightly depressed, forming a narrow, indistinct sulcal depression, the ventral end of which is curved anteroventrally in most species. The anterior boundary of the sulcal depression is formed by the posterior margin of the preadductorial node and usually rather distinct. Posteriorly this depression merges gradually into the general surface of the postadductorial area. Thus the sulcal depression can, in most species at least, be characterized as a semisulcus behind the preadductorial node. In the species studied a small, rounded adductorial muscle scar is situated at about the mid-height of the lateral surface of the domicilium or slightly ventrally of it (cf. Figs. 26 C, D, 32). It is conspicuous by the absence of the ornamentation.

Tecnomorphs with a moderately broad to narrow velar flange, not quite reaching the posterior cardinal corner. In heteromorphs the velar structure is expanded almost along its whole extension into a broad and usually rather convex dolon. The posterior end of the dolon is as a rule fairly indistinct, the convex part of the velum decreasing gradually in width in posterior direction and merging into a faintly concave velar flange of the tecnomorphic type without any particularly distinct boundary. The anterior end of the dolon is distinct, being marked by an abrupt decrease in width and in convexity of the velar structure, and by the steeply sloping area of contact between the dolon and the domicilium. The foremost part of the dolon is usually the broadest. The contact area between the dolon and the domicilium is placed considerably

higher up the side than that between the corresponding part of the tecnomorphic velar structure and the domicilium, and lies highest near the anterior end of the dolon, just in advance of the abrupt curve of the velar contact area towards the free margin. These characters of the dolon are exhibited by all heteromorphs studied of *Levisulculus*, and thus seem to be of generic value.

All species of *Levisulculus* known so far are rather small, and owing to the difficulties in their preparation the closure of the carapace along the free margin and the subvelar field are incompletely known.

Discussion.—On account of its strongly preplete outline and the rather convex and anteriorly swollen dolon the genus described takes a somewhat isolated position within *Tvaerenellinae*. The main distinguishing features from the other tvaerenelline genera lie in the position of the muscle scar, the outline of the valve, and the shape of the dolon. All species of *Levisulculus* known so far possess a faint sulcal depression, but the genus may include also entirely non-sulcate species. *Primitiella pulex* Öpik, 1937, is nonsulcate, but has the distinctly preplete outline of the valves characterizing the species included here in *Levisulculus*. Of this species only tecnomorphs are known at present. If, however, the species should possess a muscle scar situated as in *Levisulculus*, and if the heteromorphs should prove to have the *Levisulculus* type of dolon, the species may have to be referred to this genus. In this case *Levisulculus* and *Tvaerenella* are clearly distinguished also by the outline of the valves. At present *Primitiella pulex* is tentatively referred to *Tvaerenella*.

Occurrence.—All known species of *Levisulculus* occur in the *Ludibundus* limestone and contemporaneous beds. At present the genus is unknown outside Baltoscandia.

Levisulculus lineatus n. sp.

Pl. VIII, Figs. 12–15; Text-fig. 26C, D.

Holotype.—Left heteromorphic valve, UM no. T 89, figured on Pl. VIII, Fig. 12.

Type Region.—Tvären area. Found in erratic boulders.

Type Stratum.—Lowermost *Ludibundus* limestone.

Derivation of the Name.—The name refers to the ornamentation consisting of narrow ridges.

Diagnosis.—Length of the heteromorphs 0.75–0.90 mm. Sulcal depression faint, preadductorial node indistinct, situated near the ventral end of the sulcal depression. The ornamentation consists of anastomosing ridges, directed anteroventrally in front of the sulcus, and posteroventrally behind the sulcus.

Material.—2 tecnomorphs, 5 heteromorphs.

Description.—Outline rather strongly preplete, anterior end broadly rounded, posterior end almost straight. Angle of posterior cardinal corner about 90°. Valves moderately convex in ventral view, highest convexity slightly behind the sulcal depression (Pl. VIII, Fig. 13). Sulcal depression faint,

slightly curved, reaching to about $^1/_2$ of the height of the valve, rather broad and poorly defined dorsally, narrow and more distinct ventrally. A faint elevation in front of the ventral part of the sulcal depression corresponds to the preadductorial node. A similar faint elevation is situated behind the dorsal part of the sulcal depression. At the ventral end of the depression a small, rounded, smooth muscle scar, situated at about the mid-length of the lateral surface of the domicilium (cf. Fig. 26 C, D).

Tecnomorphs with a velar flange resembling that of *L. troedssoni* (cf. Fig. 26 D). Anteriorly the flange reaches to the anterior cardinal corner, posteriorly it seems to become obsolete on approaching the posterior end of the valve.

In heteromorphs the anteroventral and ventral part of the velar structure is expanded and rather strongly convex, forming a distinct dolon. The greatest width of the dolon lies anteriorly; in posterior direction the dolon narrows gradually. Anterior end of the dolon marked by an abrupt change in convexity and in the width of the velar structure, imparting to the end of the dolon a swollen appearance. Dorsally of the anterior end of the dolon and up to the anterior cardinal corner the velar structure continues as a narrow flange (cf. Fig. 26 C), identical with that of tecnomorphs. Contact area between the dolon and the domicilium strongly curved dorsolaterally, lying highest anteriorly. At the anterior end of the dolon the contact area slopes rather steeply towards the free margin. Posteriorly, near the posterior end of the valve, the narrowed dolon merges without any clear boundary into a narrow, faintly concave velar flange of tecnomorphic type. A distinct keel runs at about the middle of the dolon in its whole extension, but is most conspicuous anteriorly, and present on all heteromorphic specimens studied.

The ornamentation consists of anastomosing ridges, directed in front of the sulcal depression anteroventrally, and behind it posteroventrally, extending from the dorsal margin to the velum. The ridges cross the sulcal depression without any apparent change in direction or strength. Only the small, rounded muscle scar is uncovered by the ornamentation (Fig. 26 C, D). The external surface of the dolon is faintly radially striated.

DIMENSIONS.—See Table 23.

DISCUSSION.—The ornamentation of *L. lineatus* seems to resemble that of *Ectoprimitia corrugata* (KRAUSE). In the latter species, however, according to the description by KRAUSE (1892, p. 386), the ridges arrange themselves ven-

Table 23.

No.	UM Mus. cat. no.	L. valve	H. valve	H-L	Valve	Remarks
1	T 89	~0.89	0.52	—	h—l	Holotype. Pl. VIII, Fig. 12.
2	T 90	—	0.51	—	h—l	Figured on Pl. VIII, Figs. 13–14.
3	T 91	0.79	0.47	0.66	h—r	Figured on Pl. VIII, Fig. 15.

trally into a reticulate pattern and, according to the KRAUSE's figure the direction of the ridges is posteroventral in front of, and anteroventral behind the sulcal depression, i.e. exactly contrary to that in *L. lineatus*. Also the outline of *E. corrugata* is rather different.

OCCURRENCE.—*Levisulculus lineatus* n. sp. has been found only in the boulders on Ringsö, Tvären area, Södermanland. Lowermost *Ludibundus* limestone.

Levisulculus troedssoni (THORSLUND, 1940)

Pl. VIII, Figs. 16–18; Text-fig. 32 A.

1940 *Primitia troedssoni* n. sp.—THORSLUND, pp. 163–164, Pl. 1, Figs. 13–14.
cf. 1940 *Primitia troedssoni* n. sp.—THORSLUND, Pl. 1, Fig. 15.

HOLOTYPE.—Right tecnomorphic valve, UM no. T 10, figured by THORSLUND 1940, Pl. 1, Figs. 13–14.

TYPE REGION.—Tvären area, Södermanland. Found in erratic boulders.

TYPE STRATUM.—Lowermost *Ludibundus* limestone.

DIAGNOSIS.—Preadductorial node flattened but fairly conspicuous, sulcal depression shallow, narrow, and curved. The ornamentation consists of a faint, but distinct reticulation and, on some specimens at least, also of small scattered tubercles.

MATERIAL.—10 tecnomorphic valves.

DESCRIPTION.—Outline distinctly preplete. Lateral surface rather flattened in ventral view (cf. THORSLUND 1940, Pl. 1, Fig. 14), highest convexity slightly in front of the sulcal depression. Dorsum low, plane, epicline, its inner boundary formed by a sharp edge. Preadductorial node rather distinct, flattened, situated comparatively close to the dorsal margin, merging in anterior direction into the general surface of the preadductorial area. Sulcal depression shallow, fairly distinct, narrow, curved; anterior boundary formed by the convexity of the preadductorial node, posteriorly merging without any distinct boundary into the general surface of the postadductorial area, thus developed as a semisulcus. A small, rounded, smooth adductorial muscle scar is situated ventrally of the ventral end of the sulcus, at about the mid-height of the lateral surface of the domicilium (cf. Fig. 32 A).

Tecnomorphs with a narrow velar flange (cf. Pl. VIII, Fig. 17; on the holotype figured by THORSLUND, 1940, Pl. 1, Fig. 13 the peripheral part of the flange is broken off). Posteriorly the velar flange does not seem to reach the posterior cardinal corner, but becomes apparently obsolete on approaching the posterior end of the valve. Anteriorly the flange can be followed almost up to the anterior cardinal corner. Close to the domicilium the lateral surface of the flange is as a rule faintly undulate.

The heteromorphic valve from the Lockne area, Jämtland, figured by THORSLUND (1940, Pl. 1, Fig. 15) does not show any trace of a reticulation, and its identity with *L. troedssoni* is, therefore, uncertain. For the time being

this specimen will be referred to as *L.* cf. *troedssoni*. In this specimen the dolon has anteriorly on the whole the same swollen shape as in *L. lineatus*, the contact line between the dolon and the domicilium being abruptly bent down to the level of the narrow tecnomorphic type of the velar structure. Posteriorly the dolon merges more or less gradually into a slightly concave velar flange. In the boulders of the Tvären area no heteromorphs of *L. troedssoni* have so far been found.

Right valve with a distinct marginal ridge (cf. THORSLUND 1940, Pl. 1, Fig. 15). The subvelar field of the left valve has not been accessible to examination.

The ornamentation consists of a faint reticulation (cf. Pl. VIII, Fig. 18). Ventrally of the sulcal depression the rows of pits are directed longitudinally, behind the sulcus posterodorsally, and in front of it anterodorsally. In addition to the reticulation also scattered tubercles can be seen on some specimens (cf. Pl. VIII, Fig. 16). In other respects these specimens do not seem to differ from those which exhibit only a reticulation.

DIMENSIONS.—See Table 24. The specimens measured have been found in erratic boulders of the Tvären area, Södermanland.

Table 24.

No.	UM Mus. cat. no.	L. valve	H. valve	H-L	Valve	Remarks
1	T 274	0.86	0.51	—	t—l	Figured on Pl. VIII, Fig. 16.
2	T 10	0.79	~0.43	0.71	t—r	Holotype. THORSLUND 1940, Pl. 1,
3	T 94	0.79	0.41	—	t—r	Figs. 13–14.
4	T 92	0.76	0.45	0.68	t—l	Figured on Pl. VIII, Figs. 17–18.
5	T 93	0.66	0.36	0.60	t—l	

DISCUSSION.—*Levisulculus troedssoni* resembles *L. extraria* (ÖPIK) with regard to the shape of the sulcus and the preadductorial node. It is difficult to get a clear idea of the details of the ornamentation in the latter species as the ornamentation cannot be clearly seen in ÖPIK's figure (1937, Pl. X, Fig. 19); according to his description (1937, p. 18) it is lineate and minutely granulate, thus apparently of the same type as in *L. troedssoni*. A new figure showing the details of ornamentation is needed in order to give a better characterization of *L. extraria*. According to our present knowledge *L. troedssoni* differs from *L. extraria* essentially by the outline of the valve which in the latter species has a considerably more pronounced preplete shape.

OCCURRENCE.—*Levisulculus troedssoni* has been found only in the *Ludibundus* limestone. Södermanland, Tvären area, boulders. Similar, possibly conspecific specimens occur in Jämtland, Brunflo-Lockne area (exposure 0.7 km SSW of the Tandsbyn railway station).

Levisulculus granulosus (Thorslund, 1940)

Pl. VIII, Fig. 19; Text-fig. 32 B.

1940 *Primitia granulosa* n. sp.—Thorslund, p. 164, Pl. 1, Fig. 16.

Holotype.—Right tecnomorphic valve, UM no. T 11, figured on Pl. VIII, Fig. 19; Thorslund 1940, Pl. 1, Fig. 16.

Type Region.—Tvären area, Södermanland. From an erratic boulder.

Type Stratum.—Lowermost *Ludibundus* limestone.

Diagnosis.—Similar to *L. extraria* (Öpik), but with rather coarse tubercles and a more conspicuous sulcal depression.

Description.—Only the holotype is known. Outline distinctly preplete, posterior margin of the valve broadly rounded. Lateral surface of the domicilium moderately convex, highest convexity in front of the preadductorial node. Dorsum moderately high (tr.), faintly epicline. Preadductorial node small, distinct, smooth, rounded, situated in front of the dorsal part of the sulcal depression, its dorsal and posterior boundaries well defined, anterior and ventral boundary formed by a faint change in convexity. On account of its smooth surface the preadductorial node is, however, rather sharply defined also along its anterior and ventral margins. Sulcal depression fairly distinct, shallow, slightly curved, more or less transversally directed, extending almost to the ventral margin of the lateral surface of the domicilium. It is broadest at about halfway between the preadductorial node and the ventral end of the depression, and is provided there with a smooth, rounded adductorial muscle scar (Fig. 32 B) which is not quite clearly visible in the photograph (Pl. VIII, Fig. 19). The scar is situated at about the mid-height of the lateral surface of the domicilium. Velar structure developed as a narrow flange. Anteriorly the flange reaches almost up to the anterior cardinal corner, posteriorly it becomes rather suddenly obsolete before reaching the posterior end of the valve.

The ornamentation consists of rather coarse tubercles and a minute granulation between the tubercles. The intervals between the tubercles are usually larger than their diameter. The lateral surface of the frill is faintly undulate close to the domicilium, and covered with a fine, concentric striation.

Dimensions of the Holotype.—Length of the lateral surface of the domicilium 0.86 mm; height of the lateral surface of the domicilium 0.45 mm; height of the valve 0.53 mm.

Discussion.—The outline and the shape of the preadductorial node of *L. granulosa* resemble those of *L. extraria* Öpik. The sulcal depression seems, however, to be longer than in the latter species and the ornamentation to consist of much coarser tubercles without any trace of a reticulation.

Occurrence.—See the type region and the type stratum.

Gen. *Hesperidella* Öpik, 1937

Type Species.—*Primitia esthonica* Bonnema, 1909.

Diagnosis.—Unisulcate, with a large, rounded presulcal knob and a conspicuous crest around the sulcus and the knob. Dorsal plica strongly developed. Velar structure moderately broad, flange-like, slightly concave in tecnomorphs, anteroventral part expanded into a plane to slightly convex dolon in heteromorphs.

Species.—*Primitia esthonica* Bonnema, 1909
Primitia (*Ctenobolbina*?) *globifera* Krause, 1892.

According to Sarv (1955) a new species of *Hesperidella* occurs in the Rakvere Stage of Estonia.

Remarks.—The heteromorphic type of *Hesperidella* was previously unknown. From the other tvaerenelline genera *Hesperidella* differs clearly by its large and prominent presulcal knob, and the strong crest around the sulcus and the knob.

Occurrence.—*Hesperidella* is known from the Middle Ordovician Kukruse, Idavere, and Jõhvi Stages of Estonia, from corresponding beds in Sweden, and from the Upper Ordovician Rakvere Stage of Estonia.

Hesperidella esthonica (Bonnema, 1909)

Pl. VI, Figs. 1–3; Text-fig. 33.

1909 *Primitia esthonica* n.sp.—Bonnema, p. 32, Pl. VI, Fig. 30.
? *1924* *Primitia esthonica* Bonn.—Kummerow, p. 440.
1934 *Eurychilina esthonica* (Bonnema)—Bassler & Kellett, p. 314.
1937 *Hesperidella estonica* (Bonnema)—Öpik, p. 49, Pl. XI, Figs. 14–15.
1940 *Hesperidella globifera* (Krause)—Thorslund, p. 179, Pl. 3, Fig. 12, Pl. 5, Fig. 6.
1955 *Hesperidella estonica* (Bonnema)—Sarv, p. 16.
1956a *Hesperidella estonica* (Bonnema)—Sarv, p. 49.

Lectotype.—Right tecnomorphic valve, TM no. Os-2218, figured by Bonnema 1909, Pl. VI, Fig. 30.

Type Locality.—Kukruse (="Kuckers"), Estonia.

Type Stratum.—Kukruse Stage, probably its lower zone ($C_{II}\alpha$).

Description.—No real diagnosis can at present be given, the type species being as yet the only one which is sufficiently known.

Domicilial outline almost amplete. In ventral or dorsal view the top of the presulcal knob lies highest, the highest convexity of the rest of the valve lying slightly behind the sulcus. Presulcal knob large, its transversal diameter in tecnomorphs about equal to the distance between the ventral end of the knob and the velar flange; in heteromorphs its diameter is as a rule larger than the distance mentioned. This is due to the more dorsal position of the contact area between the dolon and the domicilium. The knob is evenly rounded or

A B

Fig. 33. *Hesperidella esthonica* (Bonnema). Reconstructions of a tecnomorphic (A) and a heteromorphic (B) valve. A, after the specimen figured on Pl. VI, Fig. 2. B, after that on Pl. VI, Fig. 1. × 35.

slightly oblong, its transversal diameter being somewhat larger than the longitudinal. Sulcus deep, rather narrow. A distinct, prominent crest running in an even curve surrounds the sulcus ventrally, and the knob ventrally and anteroventrally. Anteroventrally of the knob the crest gradually becomes low and, in front of the knob, almost obsolete. Between the knob and the crest a narrow and shallow furrow is developed which seems to be of ornamental character, not forming any conspicuous internal elevation. On the internal mould the anterior boundary of the knob is as a rule formed by a semisulcus. A shallow furrow separates the knob also from the dorsal plica, and thus the whole knob is surrounded by a distinct depression. The dorsal plica is divided into a posterior and an anterior arch, and as the posterior arch becomes almost completely obsolete anteriorly, just before reaching the anterior arch, both arches are not quite connected. The anterior arch forms a direct continuation of the crest behind the sulcus, surrounds the sulcus dorsally, and is anteriorly continuous with the velar structure.

Tecnomorphic velar structure moderately broad, flange-like, broadest ventrally, decreasing in width anteriorly and posteriorly. The anterior end of the flange is confluent with the dorsal plica, whereas posteriorly the flange ends rather abruptly, slightly ventrally of the mid-height of the lateral surface of the domicilium. On tecnomorphs no undulation of the lateral surface of the flange has been observed. Heteromorphs with a conspicuously expanded anteroventral part of the velar flange forming a faintly convex dolon surrounded by narrow, upturned, rim-like peripheral margin. In all heteromorphs examined the surface of the dolon is faintly, but distinctly undulate.

The subvelar field is slightly concave, rather high (tr.) ventrally. On the left valve a faint marginal ridge has been observed shaped as an unconspicuous thickening of the valve at the free edge. Subvelar field on the right valve not observed, closure of the carapace along the free edge unknown.

The whole lateral surface of the valve, excepting the part surrounded by the crest, is covered with minute, closely placed granules which are separated by rather deep and distinct minute depressions. This ornamentation is on the whole of a reticulogranulate type, the arrangement of the granules giving a

finely reticulate appearance. In addition there is a small number (35–60) of rather large scattered tubercles. On less well preserved valves the minute granules cannot be seen, and the ornamentation then seems to consist of tubercles only. The changing appearance due to weathering of the ornamentation in this species was pointed out also by THORSLUND (1940, p. 179). According to the observations of the present writer the reticulate appearance of the ornamentation is seen only in well-preserved specimens, not in weathered ones as stated by THORSLUND.

DIMENSIONS.—See Table 25. All specimens measured have been found in erratic boulders of Tvären area, Södermanland.

Table 25.

No.	UM Mus. cat. no.	L. valve	H. valve	H-L	H. domic.	Valve	Remarks
1	T 134	1.15	0.79	—	0.67	h—r	Figured on Pl. VI, Fig. 1.
2	T 135	1.16	0.76	—	~0.61	h—r	
3	T 136	1.13	0.74	0.95	0.68	t—r	Figured on Pl. VI, Figs. 2–3.
4	T 137	~1.08	0.72	—	0.65	t—l	
5	T 138	~1.07	—	—	0.65	t—l	
6	T 139	~1.01	—	—	0.63	t—r	
7	T 30	~1.01	—	—	0.62	t—r	THORSLUND 1940, Pl. 3, Fig. 12.
8	T 140a	~0.94	~0.61	—	0.56	t—r	

DISCUSSION.—*Hesperidella esthonica* was considered by THORSLUND (1940, p. 179) to be a junior subjective synonym to *H. globifera* (KRAUSE), the differences between the specimen figured by KRAUSE (1892, Pl. XXII, Fig. 9) and the Estonian and Swedish material, according to him, being due to differences in the state of preservation. These species may be identical, but as the figure and description given by KRAUSE (1892) are too summary to allow of a close comparison, and as his original specimen appears to be lost, there is no possibility to prove the point. At the time being it is, therefore, best to regard *H. globifera* as a nomen dubium.

OCCURRENCE.—In Estonia *H. esthonica* occurs according to SARV (1956a) in the Kukruse (C_{II}) and Jõhvi (D_I) Stages, and in the upper zone of the Idavere Stage ($C_{III}\beta$). In Sweden this species has been recorded only from the *Ludibundus* beds. The present writer has found in the surrounding facies of the Kullsberg limestone of the Siljan district some tecnomorphs of *Hesperidella* close to, or possibly identical with, *H. esthonica*, but as their state of preservation is poor a safe specific determination cannot be attempted at present.

Estonia (cf. SARV 1956a). *Södermanland*, Tvären area, erratic boulders (3 heterom., 9 tecnom.). *Jämtland* (cf. THORSLUND 1940, pp. 49, 179 as *H. globifera*).

Subfamily uncertain

Gen. *Bolbina* Henningsmoen, 1953

Type Species.—*Bollia ornata* Krause, 1896 (not *Entomis variolaris* Bonnema, 1909, as stated by Henningsmoen 1953b, p. 49).

Diagnosis.—Unisulcate, S2 broad (long.), deep, usually extending over half the height of the lateral surface of the domicilium, more or less straight and transversal, ventral end in some species slightly curved anteroventrally. Ventral part of the postadductorial area swollen, forming a distinct posteroventral lobe, posteriorly and dorsally defined by a semisulcus; a similar but less distinct anteroventral lobe present in most species. Both lobes merge into each other ventrally of the ventral end of S2. Lateral surface of the domicilium usually surrounded by a distinct furrow along the free margin. Tecnomorphs with a narrow, often rounded velar ridge; heteromorphs ventrally and anteroventrally with a moderately broad, in some species strongly convex velar flange which is usually more or less constricted in the middle.

Species.—*Bollia major* Krause, 1892
Bollia minor Krause, 1892
Bollia minor var. *ornata* Krause, 1896
Bollia minor var. *kuckersiana* Bonnema, 1909
Bollia minor var. *robusta* Bonnema, 1909
Bollia ornata var. *latimarginata* Bonnema, 1909
Ctenobolbina? *minor mitis* Öpik, 1937
Bolbina rakverensis Sarv, 1956.

Bolbina tuberculata Henningsmoen, 1954b, certainly does not belong to this genus. It seems to be a sigmoopsid species (possibly a *Lomatobolbina*?). According to Sarv (1956a, p. 46) *Bollia minor* var. *kuckersiana* Bonn., *B. minor* var. *robusta* Bonn., and *Ctenobolbina*? *minor mitis* Öpik are conspecific with *B. latimarginata*. This opinion requires, however, further confirmation, and appears rather unlikely to the present writer.

Bolbina minor var. *ornata* (Krause, 1896) is apparently not conspecific with the species described by Bonnema (1909) as *Bollia ornata*. *Bolbina ornata* (Krause) (lectotype: left valve figured by Krause 1896, Pl. XXV, Fig. 5, designated herein) is according to Krause's description and figures much larger (length 2.55 mm, height 1.53 mm, cf. Krause 1896, p. 936) than the species from the Kukruse Stage of Estonia described by Bonnema as *Bollia ornata* (length 1.28 mm, height 0.73 mm, cf. Bonnema 1909, p. 61). In stating that his measurements of *B. ornata* were taken on comparatively small specimens Bonnema (op. cit.) obviously compared his material with the specimen figured by Krause. Much larger specimens than those figured by Bonnema have evidently never been found in the Kukruse Stage of Estonia. Bonnema also

pointed to the possibility that the specimens described by him as *B. ornata* and *B. ornata latimarginata* might represent dimorphs of one species. An examination of specimens of these two types has confirmed BONNEMA's assumption, and the specimens of *B. ornata latimarginata* are considered here as heteromorphs. Also these heteromorphs do not exceed the length (excl. velum) of 1.6 mm, and thus are much smaller than the (tecnomorphic) valve of *B. ornata* measured by KRAUSE. KRAUSE's figure of the lectotype of *B. ornata* reveals also other differences between this species and the Estonian specimens determined as *B. ornata* by BONNEMA. On KRAUSE's figure the anteroventral lobe extends considerably more dorsally than in the Estonian specimens, the sulcus is shorter (tr.), and also the ornamentation seems to be slightly different. If *B. ornata sensu* BONNEMA and *B. ornata latimarginata* are regarded as conspecific the Estonian species should be called *Bolbina latimarginata* (BONNEMA) (cf. also SARV 1956a, p. 46).

DISCUSSION.—Specimens of 6 different species of the genus *Bolbina*, including some new species, have been examined by the present writer. In some characters this genus exhibits a rather considerable intraspecific variation and it is possible that future studies may necessitate its subdivision into subgenera or even a splitting into several genera. On that account no proper discussion of the generic characters of *Bolbina* will be given in the present paper.

The presence of a dimorphism in *Bolbina* was suggested already by BONNEMA (1909, p. 63), and this assumption has been confirmed by the examination of the material at the present writer's disposal. *Bolbina* evidently possesses a velar dimorphism of the general piretellid type. In tecnomorphs the velar structure is developed as a rather narrow, often rounded ridge, and in heteromorphs as a moderately broad (tr.) and long flange forming a dolon. The dolon is usually widest posteroventrally, slightly constricted at the middle of its ventral margin, and expands again anteroventrally. The constriction of the dolon in the middle may be complete, as in *Bolbina* sp. B described below (Pl. V, Fig. 20), and in this case two separate "pouches" connected by a velar ridge of tecnomorphic type are formed. In some species, as for instance in *B. latimarginata*, the dolon is moderately convex and rather broad (cf. BONNEMA 1909, Pl. IV, Figs. 9–11), but in some other species it is narrower and strongly curved, as in *Bolbina* sp. A (Pl. V, Figs. 18–19). In the latter case it is possible that the free edges of the dolon are in contact in closed carapaces. The contact area between the dolon and the domicilium seems to occupy on the whole the same position on the domicilium as the corresponding part of the contact area between the velar ridge and the domicilium in tecnomorphs. The velar structure is solid without any trace of internal partitions.

HENNINGSMOEN (1953a, p. 228) asserted that the posteroventral lobe in *Bolbina* "may end in a spur-like conical process, and appears to be dimorphic". This statement is obviously due to some mistake. No spur-like process on the posteroventral lobe has been described in any species referred by HENNINGS-

MOEN to *Bolbina*, and no such structure has been observed in the material examined by the present writer. Consequently, no dimorphism of this kind occurs in *Bolbina*.

On account of the assumed carinal (= histial) dimorphism of the spur-like process mentioned above and also of the general similarity to *Sigmobolbina* HENNINGSMOEN referred *Bolbina* to *Sigmoopsidae*. As, however, neither a histial dimorphism, nor any histial structure is known in *Bolbina* nothing warrants the inclusion of this genus in *Sigmoopsidae*. Moreover, the general similarity between *Sigmobolbina* and *Bolbina* seems to be only superficial. The presence of a dimorphism of a solid velar structure resembles that of *Piretellidae*, and *Bolbina* is, therefore, included in the latter family. Until more material has been studied the taxonomic position of this genus within *Piretellidae* is not quite clear, and on this account *Bolbina* is referred in the present paper to as *Incertae subfamiliae*.

OCCURRENCE.—The earliest known species of *Bolbina* appears in the Middle Ordovician *Crassicauda* limestone (upper Llandeilo), and the latest species occurs in the lower part of the Upper Ordovician. Representatives of this genus have been found only in Estonia and Sweden, and in the erratic boulders of northern Germany and the Netherlands.

Bolbina sp. A

Pl. V, Figs. 18–19.

DESCRIPTION.—Only one heteromorphic valve known. Domicilium rather strongly convex. Sulcus moderately long, extending slightly over half of the valve, faintly constricted in the middle, with a broad dorsal and a rather narrow ventral part. The distance between the dorsal end of S2 and the dorsal margin of the valve is about equal to the length of the dorsal part of the sulcus. Ventral part of the sulcus without any conspicuous surrounding elevation or ridge. Preadductorial node poorly defined, lying lower than the summit of the preadductorial area in front of the node. Preadductorial area rather strongly convex, slightly swollen in front of the sulcus, the top of this elevation forming the highest point of the area. Anteroventral part of the postadductorial area strongly inflated, forming a posteroventral lobe with its highest convexity near its centre. The boundaries of the lobe are defined, except anteriorly, by a semisulcus caused by the sudden change in convexity between the steeply sloping sides of the lobe and the flattened surface of the postadductorial area adjacent to it. The semisulcus reaches the sulcus at about the longitudinal mid-line of the dorsal part of the sulcus. Anteroventrally the posteroventral lobe merges without any conspicuous change in convexity into the elevated portion of the preadductorial area.

The domicilium is surrounded along the free edge by a moderately broad velar dolon, and anterodorsally and posteriorly by a velar ridge. Anteriorly the

dolon changes into a velar ridge at about the mid-height of the valve; from this point and in dorsal direction the velar structure is shaped as a low, inconspicuous ridge which becomes obsolete slightly ventrally of the anterior cardinal corner. Posteriorly the corresponding change in the velar structure takes place at about the longitudinal line through the ventral end of the sulcus. Dorsally from that point the velar ridge is stronger than on the anterior part of the valve, and extends apparently up to the posterior cardinal corner. The boundary between the velar structure and the lateral surface of the domicilium is formed by a distinct furrow which, more or less parallel to the peripheral margin of the velar ridge, can be followed up to the dorsal margin of the valve. The dolon is slightly constricted in the middle, with a moderately convex lateral and a steeply sloping ventral surface. The boundary between the lateral and ventral surfaces of the dolon is formed by a faint keel. The subvelar field has not been accessible for examination.

The ornamentation consists of about 20 rather coarse pits at the bottom of the furrow between the velar structure and the lateral surface of the domicilium, and of a small number of similar pits on the ventral slope of the posteroventral lobe. The rest of the surface of the valve appears to be smooth.

Dimensions.—Length of the valve 1.42 mm; length of the lateral surface of the domicilium 1.35 mm; length of the hinge-line 1.03 mm; height of the valve 0.79 mm; height of the lateral surface of the domicilium 0.68 mm.

Discussion.—*Bolbina* sp. A appears to belong to a new species. This species can, however, not be properly defined until more material has been found. It is on the whole rather similar to *B. latimarginata* (Bonn.), but differs e.g. by the ornamentation and the considerably greater convexity of the dolon.

Occurrence.—The specimen described has been found on Ringsö, Tvären area, in an erratic boulder from the lower *Ludibundus* limestone.

Bolbina sp. B

Pl. V, Fig. 20.

Description.—Sulcus moderately long, extending ventrally to about half the height of the valve, broadest dorsally, decreasing in width (long.) ventrally, with a rather narrow ventral end. The sulcus is slightly constricted at about its dorsal third, with a small preadductorial node in front of the constriction. The node is poorly defined, flattened, lying lower than the surface of the preadductorial area in front of the node. Preadductorial area rather strongly convex, sloping most steeply ventrally, and more gently in dorsal and anterior direction. It is slightly swollen in front of the sulcus, the top of this elevation forming the summit of the area. Anteroventral portion of the postadductorial area strongly inflated, forming a posteroventral lobe. Posteriorly and dorsally the lobe is defined by a semisulcus which is most distinct posteriorly; anteriorly the lobe merges into the general surface of the preadductorial area without any distinct boundary. The dorsal end of the lobe is situated at about the longitu-

dinal line through the preadductorial node. In ventral view the summit of the lobe lies higher than that of the preadductorial area. Dorsally and behind the lobe the postadductorial area of the valve is moderately and evenly convex. Dorsum very low, almost missing.

Velar structure developed as two moderately convex, globular flanges of about equal size, connected by a narrow ridge. Anteriorly and posteriorly the velar structure continues as a narrow ridge extending up to the cardinal corner. The globular flanges probably represent dolonal structures, and thus the specimens found are apparently heteromorphs. The subvelar field was not accessible for examination.

The ornamentation consists of a distinct row or rather coarse pits at the boundary between the velar structure and the lateral surface of the domicilium, and of similar pits on the ventral, steeply sloping part of the lateral surface of the domicilium and on the posterior part of this surface behind the posteroventral lobe. The rest of the surface of the valve appears to be smooth.

Dimensions.—Length of the valve 1.08 mm; length of the hinge-line 0.93 mm; height of the valve 0.64 mm; height of the lateral surface of the domicilium 0.55 mm.

Discussion.—The species described as *Bolbina* sp. B evidently belongs to a new species, but as the tecnomorphic type is unknown this species cannot be properly defined at present. It is quite unique among *Bolbina* as well as among other palaeocope ostracodes in having the probable dolon developed as two separate pouch-like extensions. The other characters of the species are of the general *Bolbina* type and, indeed, except for the peculiar dolon, the specimen described is rather similar to the valve described above as *Bolbina* sp. A. It differs by a slightly shorter sulcus, the details of the shape of the posteroventral lobe, which is posteriorly and dorsally more indistinctly delimited, and to some extent apparently also by details of the ornamentation.

Occurrence.—*Bolbina* sp. B has been found only in the *Crassicauda* limestone. *South Bothnian area*, erratic boulder Erken no. 10 (1 specim.). *Västergötland*, Kinnekulle, Norra Skagen bore (1 specim.).

Fam. BASSLERATIIDAE E. A. Schmidt, 1941

[*Nom. transl.* Jaanusson, herein (*ex Bassleratiinae* E. A. Schmidt, 1941)].

Diagnosis.—Velar structure formed by a solid extension of the shell, developed as a flange, a ridge, or a well-defined bend. Some early genera probably possess a velar dimorphism of a simple type. In the other genera dimorphism is not known. A carinal ridge may be present or missing. In practically all genera L2 is strongly developed, forming a lobe or a rounded knob.

Subfamilies.—*Bassleratiinae* E. A. Schmidt, 1941
Quadrijugatorinae Kesling & Hussey, 1953
? *Ctenonotellinae* E. A. Schmidt, 1941.

Discussion.—In this family two groups of genera are included as separate subfamilies; the subfamilies are believed to represent more or less natural assemblages of genera, their interrelation is, however, somewhat uncertain at present. The present writer has, nevertheless, preferred at the present state of our knowledge to classify these groups in one family than to increase the number of the palaeocope families by one more.

The features common to all these subfamilies are of a rather general nature. They all have a solid velar structure in various states of development. In *Quadrijugatorinae* some early genera probably possess a velar dimorphism, otherwise the members of *Bassleratiidae* are obviously non-dimorphic. Nearly all genera possess a strongly developed L2, mostly in form of a knob.

Bassleratiinae possess a carinal ridge and usually also other ornamental ridge-like structures or knobs of lobal character. In their arrangement no distinct quadrilobal pattern can be recognized.

Quadrijugatorinae probably are more primitive than *Bassleratiinae*. Its early genera are distinctly quadrilobate, possess a wide velum and probably also a simple type of velar dimorphism. The general trend of evolution within the subfamily goes towards the obsolescence of the lobes and the reduction of the velar structure. Some of these evolutionary changes are rather well documented (for instance in the morphological series *Tallinnellina–Rigidella–Steusloffia*).

Ctenonotella Öpik, 1937, the type genus of the subfamily *Ctenonotellinae* E. A. Schmidt, 1941, may be closely related to *Tallinnella*, as also suggested by Sarv (1955, p. 20, Table 3). The quadrilobation of *Ctenonotella* is easily recognizable, L2 and L3 developed as prominent, elongate lobes, and L1 and L4 being almost obsolete. The velar structure is fairly broad and flange-like. Until the presence or absence of a dimorphism has been ascertained, and the shape of the subvelar field is known the taxonomic position of this genus remains uncertain. It is possible that further studies may prove the subfamily *Ctenonotellinae* to be a senior synonym of *Quadrijugatorinae*.

Bassleratiidae differ from *Piretellidae* mainly by the absence of an advanced type of velar dimorphism, and also by certain persistent patterns of lobation (cf. p. 276).

Occurrence.—The earliest *Bassleratiidae* (*Quadrijugatorinae*) belong to the oldest eurychilinaceans known, appearing already in the Lower Arenig. The latest *Bassleratiinae* occur in the Middle Devonian.

Subfam. BASSLERATIINAE E. A. Schmidt, 1941

Diagnosis.—In addition to a ridge- or flange-like velar structure a strong carinal ridge is present. Lateral surface of the domicilium with a more or less distinct, mostly rounded and knob-like L2 and usually also with other knob-like elevations and ornamental ridges arranged without any distinct quadrilobate pattern. No velar dimorphism.

GENERA.—*Polyzygia* GÜRICH, 1896
Bassleratia KAY, 1934
Bellornatia KAY, 1934
Thomasatia KAY, 1934
? *Raymondatia* KAY, 1934
Ulrichia (*Kozlowskiella*) PŘIBYL, 1953
? *Kayatia* ÖPIK, 1953
Lennukella n. gen.

DISCUSSION.—The delimination of this subfamily in the present paper corresponds on the whole to that of E. A. SCHMIDT (1941, pp. 50–51). The Devonian genus *Polyzygia* has been redescribed recently by PŘIBYL (1953), KRÖMMELBEIN (1953), and ADAMCZAK (1956). The general characters of this genus seem to agree rather closely with those of the Ordovician bassleratiines. *Kozlowskiella* certainly has no relationship to *Ulrichia* as PŘIBYL thought (1953) as it possesses two distinct supramarginal ridges on both valves (cf. PŘIBYL 1953, Pl. I, Figs. 4, 16). The lower of these ridges is a velar structure, whereas the upper probably corresponds to the carinal ridge of the other bassleratiines. The lobation of *Kozlowskiella* reminds that of *Thomasatia*.

Kayatia may represent a simple unisulcate member of *Bassleratiinae*. The ventral view of a right valve of the type species (ÖPIK 1953, Pl. XI, Fig. 107) has decidedly the appearance of a bassleratiine. The transverse section through the carapace of *K. prima* as given by ÖPIK on Text-fig. 12 may not be quite correct as it would evidently differ considerably from a corresponding section through the valve figured by ÖPIK on Pl. XI, Fig. 107, particularly by the absence of a subvelar field. If ÖPIK's figure of the transversal section is correct *Kayatia* would, by its strongly asymmetrical development of the ornamental ridges, be rather unique among eurychilinaceans. In *Raymondatia* the presence of a velar structure has not been proved so far, and for this reason this genus is only tentatively included in *Bassleratiinae*.

OCCURRENCE.—*Lennukella europaea* seems to be the earliest bassleratiine species known up till now, appearing already in the Upper Llandeilo of Baltoscandia. Other Ordovician genera are North American (cf. KAY 1934, 1940). *Polyzygia* has been reported from the Middle Devonian of the central Devonian field of U.S.S.R. (POLENOVA 1952), Poland (cf. PŘIBYL 1953, ADAMCZAK 1956), and the Eifel mountains, Germany (KRÖMMELBEIN 1953). *Kozlowskiella* occurs in the Middle Devonian of Poland (PŘIBYL 1953). A further Middle Devonian bassleratiine is "*Drepanella*" *orvikui* ÖPIK, 1935, from the Old Red Sandstone of Estonia.

Gen. *Lennukella* n. gen.

TYPE SPECIES.—*Drepanella europaea* ÖPIK, 1937.

DERIVATION OF THE NAME.—From *Lennuk*, the name for a ship in Estonian mythology.

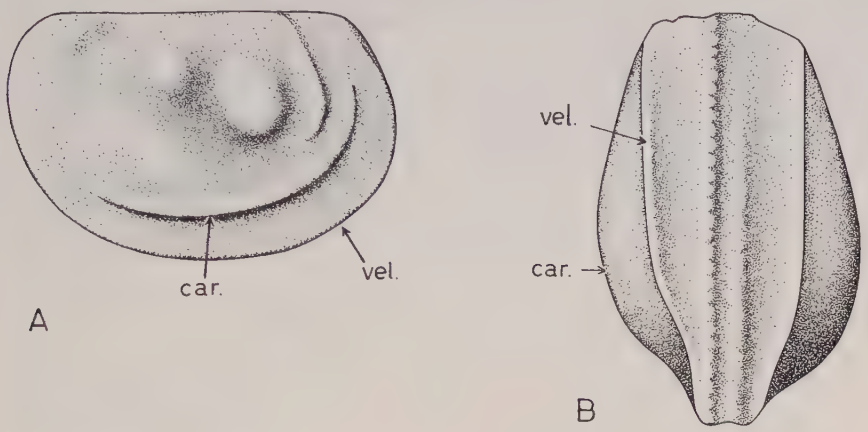


Fig. 34. *Lennukella europaea* (Öpik). Reconstruction of the lateral view (A) after the specimen figured on Pl. X, Fig. 1, and ventral view (B) after Öpik 1937, Pl. III, Fig. 12b. × 30. *Vel.*, velar ridge; *car.*, carinal ridge.

Diagnosis.—Unisulcate, with a large preadductorial knob in front of, and a considerably smaller knob behind S1. Dorsal ridge fairly strong, continuing anteriorly in an ornamental ridge situated in front of the preadductorial knob. Lateral surface of the valve surrounded ventrally and anteroventrally by a strong carinal ridge. Area between carinal and velar ridges rather broad and more or less plane. Velar structure developed as a narrow ridge concealing the subvelar field in lateral view. Subvelar field fairly high (tr.). Equivalved, in the type species with a row of coarse marginal tubercles.

Discussion.—Only the type species is known so far. As pointed out by E. A. Schmidt (1941, p. 51) *Drepanella europaea* has a distinct velar structure, and on this account cannot be included in the genus *Drepanella*. He placed it in *Bassleratia*, but the arrangement of the knobs and ridges of this species differs rather considerably from that of *Bassleratia typa* Kay. Henningsmoen (1953a, p. 220) suggested that the general arrangement of the lobes and ridges in *L. europaea* reminds of that of *Steusloffia* and included this species in the latter genus. However, *Steusloffia* has no carinal ridge in the sense of the present writer, and the similarities between *L. europaea* and *Steusloffia* in the ornamental and lobal characters are of a fairly general nature, without suggesting any close affinity. On account of the presence of a distinct carinal ridge *L. europaea* is included here in the *Bassleratiinae*. The development of the ornamental and lobal characters in this species differs, however, distinctly from the other bassleratiine genera, and a new genus is, therefore, erected.

Within *Bassleratiinae Lennukella* displays the greatest resemblance to *Bassleratia*, but differs by the only ventrally and anteriorly developed carinal ridge, the absence of a distinct ridge ventrally of S1, and several other characters. It should, however, be noted that the ventral views of the carapace of *Lennu-*

kella and *Bassleratia* are fairly similar (compare Öpik 1937, Pl. III, Fig. 12b and Kay 1934, Pl. 46, Fig. 9).

Occurrence.—The type species of *Lennukella* has been found in the lower Middle Ordovician (Llandeilo and the lowermost Caradoc) of Estonia and in the South Bothnian area of Sweden.

Lennukella europaea (Öpik, 1937)

Pl. X, Fig. 1; Text-fig. 34.

1937 *Drepanella europaea* n.sp.—Öpik, p. 54, Pl. III, Figs. 11a–12d, Pl. VIII, Figs. 10a, 10b, Pl. XII, Figs. 2–3.
1941 *Bassleratia europaea* (Öpik)—E. A. Schmidt, p. 51, Pl. 5, Figs. 41a, c, d (copied from Öpik 1937).
1953a *Steusloffia europaea* (Öpik)—Henningsmoen, pp. 219–220, Text-fig. 8b (after Öpik 1937, Pl. III, Fig. 11a).
1955 *Steusloffia europaea* (Öpik)—Sarv, p. 16.
1956a *Steusloffia europaea* (Öpik)—Sarv, p. 52.

Holotype.—A complete carapace, figured by Öpik 1937, Pl. III, Fig. 12a–d (TM).

Type Locality.—Estonia, Lasnamägi, exposure close to the "South Lighthouse".

Type Stratum.—Uhaku Stage (C_1c).

Discussion.—Only the type species being known so far its diagnosis coincides largely with that of the genus *Lennukella*. This species has been well illustrated by Öpik (1937), and the Swedish specimens do not contribute to the knowledge of its characters.

Occurrence.—In Estonia *L. europaea* has been found in the Uhaku Stage and in the Kukruse Stage ($C_{II}\alpha$ according to Sarv 1956a, p. 52). *South Bothnian area.*—Erratic boulder Bergsbrunna no. 1, derived probably from the uppermost *Crassicauda* beds (2 specim.).

Subfam. QUADRIJUGATORINAE Kesling & Hussey, 1953

Diagnosis.—The velar structure developed as a flange or a ridge, in some genera merely as a sharp edge. Some early genera probably possess a velar dimorphism of a simple type, the contact area between the velar structure and the domicilium showing an identical position in both dimorphs. Other genera without velar dimorphism. Carinal ridge absent. All genera known so far are quadrilobate, or have evidently developed from quadrilobate ancestors by the obsolescence of some lobes.

Genera.—*Ceratopsis* Ulrich, 1897
Steusloffia Ulrich & Bassler, 1908
Kiesowia Ulrich & Bassler, 1908

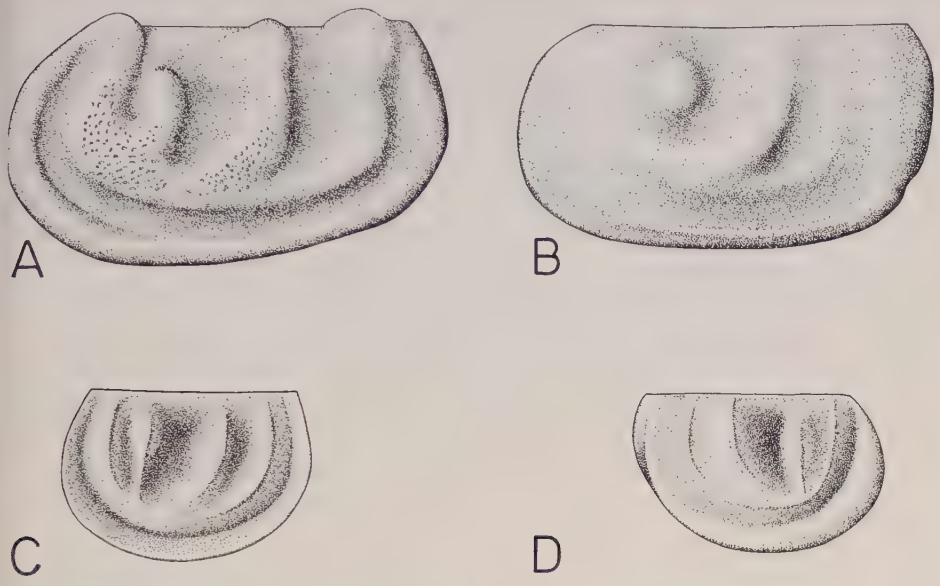


Fig. 35. Reconstructions of *Tallinnella dimorpha* Öpik (A), *Tallinnella sebyensis* n.sp. (B), *Tallinnellina lanceolata* (Hessl.) (C), and *Rigidella mitis* (Öpik) (D). A, after the specimen figured on Pl. IX, Fig. 1. B and C after the holotypes. D, after the probably heteromorphic valve figured on Pl. X, Fig. 5. × 35.

Tallinnella Öpik, 1937
Rigidella Öpik, 1937
Pseudostrepula Öpik, 1937
Quadrijugator Kesling & Hussey, 1953
Quadrilobella V. Ivanova, 1955
? *Trilobella* V. Ivanova, 1955 (non Woodward, 1924)
Protallinnella nov.
Tallinnellina nov.

There occur in addition several species which cannot be classified with the existing genera, but which require further study before the new genera can be erected.

Discussion.—For *Tallinnella dimorpha*, *Protallinnella*, *Rigidella*, and *Tallinnellina* the presence of a velar dimorphism has been suggested. The other genera referred to this subfamily evidently do not exhibit any dimorphic change of the velar structure. In *Steusloffia* which has originated almost certainly from *Rigidella*-like ancestors (cf. p. 357) the ability to produce a velar dimorphism may have been lost in the course of evolution.

The genera included here in *Quadrijugatorinae* were classified by Henningsmoen (1953a) partly as *Tetradellidae* and partly as *Bassleratiinae*; one genus was included by him with some doubt in *Sigmoopsidae* (*Kiesowia*). As pointed out by Kesling & Hussey (1953) *Tetradellidae* should be restricted to genera with the locular type of dimorphism differing from loculate hollinids by certain

details of lobation. In this delimination the tetradellids have been transferred in the present paper to *Hollinacea*. For other quadrilobate genera, thought by KESLING & HUSSEY to be non-dimorphic, the family *Quadrijugatidae* [= recte *Quadrijugatoridae*] was erected by them. In this family they included, in addition to the species which in the present paper are regarded as belonging to *Tallinnellina* [*T. lanceolata* (HESSL.)] and *Protallinnella* [*P. grewingki* (BOCK)], also *Ceratopsis* and *Quadrijugator*, and, furthermore, the sigmoopsid genera *Ogmoopsis* and *Glossopsis* (= *Glossomorphites*).

Steusloffia, *Rigidella*, and *Pseudostrepula* were placed by HENNINGSMOEN (1953a) into *Bassleratiinae*, apparently on account of certain similarities of lobal and ornamental characters between these genera and the other *Bassleratiinae*. A close study of the representatives of these genera has, however, shown that this similarity is of a fairly general nature, and does not afford any real evidence of relationship. There exists on the other hand a rather close phylogenetic connection between them and *Tallinnella*-like genera as recognized also by HENNINGSMOEN. The specimens of *Kiesowia* studied by the present writer show that this genus has a flattened velar structure, resembling that of certain species of *Tallinnella*. In some species at least the outer part of this structure is developed as a row of spines. The subvelar field is low (cf. ÖPIK 1937, Pl. XIV, Fig. 2); a quadrilobation similar to that of *Tallinnella* is clearly discernible. At the present state of our knowledge this genus seems in all probability to be a specialized off-shoot from *Tallinnella*-like forms. It is certainly no sigmoopsid.

As pointed out in the diagnosis, all genera referred here to *Quadrijugatorinae* are quadrilobate or have evidently developed from quadrilobate ancestors. *Steusloffia*, e.g., may be characterized as unisulcate and bilobate, but is linked to the quadrilobate *Tallinnellina* through a rather continuous morphological series, and the original quadrilobation is in fact rather clearly traceable. In *Pseudostrepula* only the arrangement of the crests and the large knob-like L2 suggest a quadrilobate pattern. It is possible that further obsolescence of the lobation may have given rise to smooth unisulcate or even non-sulcate quadrijugatorines. "*Conchoprimitia*" *symmetrica* (ULRICH) (cf. KAY 1940, p. 249, Pl. 30, Figs. 28–32) is apparently such an almost non-sulcate member of *Quadrijugatorinae*.

OCCURRENCE.—The earliest members of *Quadrijugatorinae* occur already in the Arenig. No Silurian or Devonian species referable with certainty to this subfamily is known at present.

Gen. *Tallinnella* ÖPIK, 1937

TYPE SPECIES.—*Tallinnella dimorpha* ÖPIK, 1937.

DIAGNOSIS.—All species known are rather large. Quadrilobate, L2 shorter than the other lobes, united with the connecting lobe or developed as a knob. Ventral part of L1 mostly more or less swollen. Velar structure developed as

a thick ridge or a thick, narrow flange, broadest anteriorly, forming a raised or flattened border along the free margin around a part of the lateral surface of the valve. The velar ridge ends rather abruptly before reaching the posterior cardinal corner. In the type species a velar dimorphism has been described, the velar flange being broader anteriorly in heteromorphs.

SPECIES.—*Tallinnella dimorpha* ÖPIK, 1937
Beyrichia marchica KRAUSE, 1889
Beyrichia marchica angustata KRAUSE, 1891
Beyrichia marchica lata KRAUSE, 1891
Tallinnella trident HENNINGSMOEN, 1953
Tallinnella tumida HENNINGSMOEN, 1953
Tallinnella pachydactyla n.sp.
Tallinnella sebyensis n.sp.

In addition also *Beyrichia bohemica* BARRANDE, 1872, and *Tallinnella? hloubetinensis* n.sp. are tentatively included in this genus.

GENERIC CHARACTERS.—Outline slightly preplete to nearly amplete. Dorsum low, convex, almost orthocline. No dorsal plica.

Quadrilobate. L1 with a mostly swollen ventral part and a variable shape of the dorsal part which may be parallel-sided, bulbous, or in some species even obsolete. L2 shorter than the other lobes, mostly constricted ventrally, in several species separated from the connecting lobe by a shallow furrow and forming a knob. L3 with a usually bulbous dorsal part. It is the most persistent of all lobes, occurring with an essentially similar shape in nearly all species known so far and never obsolete. L4 is mostly lower than the other lobes, its dorsal part may be parallel-sided, bulbous, or in some species obsolete. It is as a rule the first of the lobes to disappear. Thus the shape of the lobes varies rather considerably within the genus. The extreme, prominent and flattened lobation seems, however, to be united by a rather continuous morphological series of intermediate types. Apparently also the trend towards obsolescence of the lobes has found expression along several different lines of development.

The velar structure forms a thick ridge or flange which protrudes mostly in lateral as well as in peripheral direction forming a border around a part of the lateral surface of the valve. Anteriorly and anteroventrally the velar structure is as a rule broader than ventrally or posteriorly, forming a flange which protrudes considerably beyond the free margin (cf. for instance Pl. IX, Figs. 4, 13; ÖPIK 1937, Pl. II, Figs. 1b, 2b). In some species with an advanced obsolescence of the lobes the lateral surface of the velar structure is flattened, and merges into that of L1 (*T. sebyensis*, cf. Pl. IX, Fig. 12). Anteriorly the velar flange reaches the anterior cardinal corner close to the free edge (cf. ÖPIK 1937, Pl. X, Fig. 1). Posteriorly the thick velar ridge ends as a rule rather abruptly before reaching the posterior cardinal corner.

Tallinnella dimorpha is equivalved with a row of marginal tubercles on either valve. In other species the closure of the carapace is unknown so far. The subvelar field is rather low.

Dimorphism is known at present only in the type species, and was described by Öpik (1937, Pl. II, Figs. 1, 2). In supposed heteromorphs of this species the velar flange is broader (long.) anteriorly, but the difference in width is not very conspicuous, especially in lateral view. The course of the contact area between the velar structure and the domicilium is identical in both dimorphs. The presence or absence of dimorphism in the other species can not be ascertained before more material has been examined. Unfortunately the material studied did not contribute to the knowledge about the probable dimorphism in the genus.

Remarks on Some Bohemian Tallinnella-like Species.—The present writer has had the opportunity of examing topotype specimens of *T.? bohemica* Barrande, 1872, and the original material of the species determined by E. A. Schmidt (1941) as *Tetradella bohemica*. The latter species is named below *Tallinnella? hloubetinensis* n.sp.

The material of *T.? bohemica* in the possession of RM and studied by the present writer comes from the type locality (cf. E. A. Schmidt 1941, p. 43; Hughes 1954, p. 41), and there is no doubt whatsoever that the specimens at the present writer's disposal are conspecific with the specimens figured by Barrande (1872, Pl. 26, Fig. 13, Pl. 34, Figs. 19–20 [= lectotype, designated by E. A. Schmidt 1941, p. 43], 21–22). Their determination is in all probability due to J. Barrande himself. The lateral view of the specimens studied and of those figured by Barrande are closely similar, except for the shape of L4 which has apparently been drawn too long by Barrande. Amongst the numerous specimens studied the lobation is remarkably constant. The interpretation of the outer part of the valve of this species by Barrande is, however, obviously not correct. There is no doubt that the outer part of the valve illustrated by him as a frill or flange is in reality the rather plane extralobate area; the moderately high (tr.) subvelar field has apparently not been observed by Barrande in this species. Also in his transversal sections (Barrande 1872, Pl. 34, Figs. 20 and 21) the subvelar field has been omitted.

In *T. bohemica* (cf. Pl. X, Fig. 3; Text-fig. 36) the velar ridge is narrow and thick, protruding about as much ventrally as laterally, and concealing in lateral view the subvelar field along the ventral margin. The velar ridge forms a narrow border around the anterior and ventral part of the lateral surface of the valve. Anteriorly the ridge extends up to the dorsal margin, reaching the latter close to the anterior cardinal corner; posteriorly it becomes obsolete slightly dorsally of the mid-height of the valve. The width of the velar ridge is almost uniform along its whole extension, and no anterior flange is developed.

Tallinnella? bohemica differs from all Baltoscandian species of *Tallinnella* by its narrow lobes, its narrow velar ridge, and especially by the absence of an

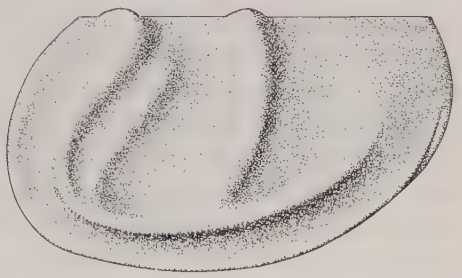


Fig. 36. Reconstruction of *Tallinnella? bohemica* (Barr.) after the specimen figured on Pl. X, Fig. 3. × 35.

expanded anteroventral flange of the velar structure. In these respects the specimens described as *Tetradella bohemica* by E. A. Schmidt (1941) occupy a somewhat intermediate position between the Baltoscandian species of *Tallinnella* and *T.? bohemica.*

As evident already from E. A. Schmidt's figures (1941, Pl. 2, Figs. 11–13) the specimens from the Bohdalec beds determined by him as *Tetradella bohemica* represent another species. This assumption could be confirmed by an examination of his material at the Senckenberg Museum, Frankfurt a.M. For the species from the Bohdalec beds the name *Tallinnella? hloubetinensis* n. sp. is here proposed. *Holotype:* carapace no. X/E 831 a (Senckenberg Museum), figured by E. A. Schmidt 1941, Pl. 2, Fig. 11. *Type locality:* Hloubetin, Czechoslovakia. *Type stratum:* Bohdalec beds (d ε 2). *Diagnosis:* Lobes moderately broad, rounded, ventral part of L1 slightly constricted, L4 long, extending to the dorsal margin, connecting lobe between L3 and L4 poorly defined; velar ridge separated from the lobate area by a faint furrow only, lateral surface of the velar structure almost plane, velar ridge narrow (tr.), reaching posteriorly to about the transversal line tangential to the posterior end of L4 or slightly in front of it.

The general lobation of *T.? hloubetinensis* resembles that of certain species of *Tallinnella.* The ventral part of L1 is, however, not expanded, but this applies alto to *T. pachydactyla.* The velar structure of *T.? hloubetinensis* is only slightly wider anteroventrally than ventrally, and does not form a wide flange (cf. E. A. Schmidt 1941, Pl. 2, Fig. 11v). In this respect this species exhibits greater similarity with *T.? bohemica* than with the Baltoscandian species of *Tallinnella.*

T.? bohemica and *T.? hloubetinensis* may be regarded as late derivatives of *Tallinnella* with a partly reduced velar structure. On the other hand, future studies may prove the existence of a whole group of similar related species dating back to Lower Ordovician. In this case these species ought to be included into a separate genus.

Discussion.—The delimination of the genus *Tallinnella* in the present paper coincides essentially with that of Öpik (1937, p. 24) and Hessland (1949, p. 338). E. A. Schmidt (1941, p. 38) considered *Tallinnella* to be synonymous with *Tetradella,* but pointed out that *Tallinnella* might be considered a sub-

genus of the latter in which subgenus he was inclined also to place "*Beyrichia*" *grewingki* Bock. Hessland (1949, p. 338) regarded the appearance of the velar structure and the shape of certain lobes as distinctive enough to consider *Tallinnella dimorpha* and related species as belonging to a separate genus. Henningsmoen (1953a, pp. 213–214) restricted the genus *Tetradella* to species with a locular dimorphism, and included in *Tallinnella* most of the quadrilobate and non-loculate species which had previously been placed in *Tetradella*. With such a delimination, however, the genus *Tallinnella* became a highly heterogeneous assemblage of quadrilobate forms. The heterogeneity of this genus as treated by Henningsmoen is most apparent if the shape of the velar structure is considered. In his sense *Tallinnella* includes forms with a wide frill-like velum, those with a velar ridge of various shape, and also forms without any trace of velar structure at all (as e.g. "*Tallinnella*" *mjoesensis* Henningsm.). As the shape of the velar structure is otherwise fairly distinctive for the eurychilinacean genera of other families, it was a priori evident that a further subdivision of the genus *Tallinnella* in the sense of Henningsmoen (1953a) would be unavoidable. A general revision of the quadrilobate *Tallinnella*-like species lies, however, outside the scope of the present paper. In addition to the typical species of *Tallinnella* only certain Lower Ordovician quadrilobate species with a wide frill are considered here. For these the new genera *Tallinnellina* and *Protallinnella* are established. *Tallinnellina* and *Protallinnella* possess a thin, broad, frill-like, entire velum, and differ from each other by the shape of the velum, the height of the subvelar field on the posterior part of the valve, etc. *Tallinnella* differs from these genera by a thick, ridge-like velar structure which posteriorly ends more or less abruptly before reaching the posterior cardinal corner, and which is mostly expanded anteriorly into a moderately broad, possibly dimorphic flange. Moreover, also some trends of lobation and of the shape of the subvelar field are distinctive to *Tallinnella*.

Occurrence.—At present the genus *Tallinnella* is known from the uppermost Lower Ordovician and the lower and middle parts of the Middle Ordovician of Baltoscandia and the North German erratic boulders. Additionally two Bohemian species are tentatively referred to this genus.

Tallinnella dimorpha Öpik, 1937

Pl. IX, Figs. 1–9; Text-figs. 35A, 37.

1937 *Tallinnella dimorpha* n.sp.—Öpik, pp. 24–25, Pl. II, Figs. 1a–1b, Pl. X, Figs. 1–2.
1947 *Tallinnella dimorpha* Öpik—Jaanusson, p. 46.
1948 *Tallinnella dimorpha* Öpik—Thorslund, pp. 344, 350, 359–360.
1951c *Tallinnella dimorpha* Öpik—Kesling, Pl. XII, Figs. 1a, b, 2a–c (after Öpik 1937).
1955 *Tallinnella dimorpha* Öpik—Sarv, p. 14.
1956a *Tallinnella dimorpha* Öpik—Sarv, p. 52.

HOLOTYPE.—Left, probably heteromorphic valve, TM no. Os-2070, figured by ÖPIK 1937, Pl. II, Figs. 2a–b.

TYPE LOCALITY.—Uhaku, Estonia.

TYPE STRATUM.—Uhaku Stage (C_1c), bed no. 5, middle part (cf. section in ÖPIK 1937, p. 3, Fig. 1).

DIAGNOSIS.—Dorsal part of L1 rather broad, usually expanded; L2 comparatively narrow and short, constricted ventrally, coalescent with L1; L3 high, constricted in the middle, dorsal part bulbous; connecting ridge between L3 and L4 low and narrow; dorsal part of L4 strongly expanded, forming a broad (long.) bulb. Velar ridge thick, forming a broad, prominent border around the lateral surface of the domicilium along the free edge; extralobal area fairly wide. L1, the connecting lobe between L1 and L2, and usually also L3 covered with large, closely spaced, deep pits. Lateral and ventral surface of the velar ridge finely granulate.

DESCRIPTION.—Outline slightly preplete. All lobes prominent. Ventral part of L1 broad (long.), expanded, narrowing dorsally; dorsal part more or less bulbous, dorsal end slightly protruding beyond the dorsal margin. The anterior end may or may not be continuous with the velar ridge. Close to its posterior margin L1 bears a distinct keel. L2 short, its length (tr.) slightly larger than the distance between the dorsal end of L2 and the dorsal margin of the valve, constricted ventrally, dorsal part forming an oblong bulb. The summit of L2 lies much lower in ventral or dorsal view than the summits of L1 and L3. Ventrally L2 is continuous with the swollen ventral part of L1. The connecting lobe between L2 and L3 is rather narrow (tr.), its summit much lower in ventral view than the adjacent ventral parts of L1 and L3. L3 high, oblong, with steeply sloping sides, slightly constricted and curved in the middle with a strong keel dorsally on anterior margin and ventrally on posterior margin. Dorsal part swollen, bulbous, dorsal end protruding beyond the dorsal margin of the valve. Connecting ridge between L3 and L4 low and narrow, ventral part of L4 only slightly wider and higher, dorsal part strongly swollen, forming a large bulb, the dorsal end of which protrudes beyond the dorsal margin of the valve.

In anterior or ventral view the highest point of the valve lies slightly dorsally of the middle of L3, at about the ventral end of the dorsal expanded part of L3. The summits of the ventral parts of L3 and of L1 lie lower, but well above the summit of the velar ridge. The velar ridge reaches higher laterally than the summit of L4 which is, therefore, hidden in strictly ventral view.

The extralobal area is more or less uniformly broad with a slightly concave bottom which lies at about the same level as that of the sulci. The lateral surface of the valve is surrounded by a broad velar ridge forming a strongly raised border. The width (tr.) of the velar ridge is about equal to or slightly less than the width (tr.) of the extralobal area. The anterodorsal end of the velar ridge reaches the anterior cardinal corner, and is usually, but not always,

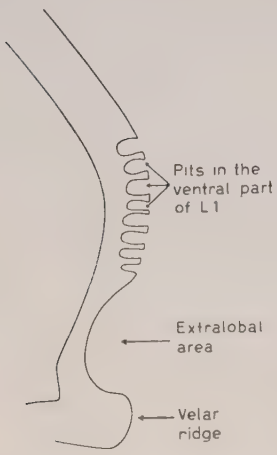


Fig. 37. *Tallinnella dimorpha* Öpik. Diagrammatic drawing of a transverse section of the valve to show the depth of the pits in the ventral part of L1. After a thin section of a specimen from the South Bothnian erratic boulder Bergsbrunna no. 1. × 40.

coalescent with L1. The posterodorsal end of the velar ridge becomes as a rule rather suddenly obsolete at about the height of the ventral end of the bulbous part of L4, and does not reach the posterior cardinal corner. A low, poorly defined, rounded ridge extending from the velar ridge up to the posterior cardinal corner is, however, occasionally developed. The outer surface of the velar ridge is rather steeply sloping posteriorly, and protrudes only slightly beyond the free edge (cf. Pl. IX, Fig. 3). Ventrally the inclination of the ridge is more pronounced, and anteriorly the ridge is flattened into a flange protruding considerably beyond the free edge. Öpik (1937, Pl. II, Figs. 1, 2; cf. also Kesling 1951c, Pl. XII, Figs. 1, 2) suggested this flange to be broader in some adult specimens and narrower in others. According to him the differences in the width of the flange are due to sexual dimorphism, the specimens possessing a narrow flange representing males (= tecnomorphs) and those with a broad flange females (= heteromorphs). Thus the broader type of flange would constitute a simple type of dolon differing from the corresponding part of the velar structure in tecnomorphs only by its width, but not by the position of the contact area between the velar structure and the domicilium. The lateral margin of the velar ridge is distinctly keeled. In ventral view this keel has its highest position posteriorly, and gradually descends in anterior direction (cf. Pl. IX, Fig. 3).

The material examined offers no conclusive evidence with regard to the presence or absence of dimorphism. The differences in the width of the velar structure between both dimorphs are rather slight, and can be fully ascertained only when the interior view of the valve is accessible for observation. In lateral view the free edge of the valve is completely concealed, and as the shape of the anterior part of the velar ridge is subject to rather considerable variation, the exact width of the flange cannot always be ascertained. It is possible also that the comparatively small number of specimens studied include only tecnomorphs or tecnomorphs and some fragmentary heteromorphs.

Table 26.

No.	UM Mus. cat. no.	L. valve	H. valve	L. lob.	H. lob.	Valve	Locality	Remarks
1	B 279	2.66	1.57	1.81	1.19	l	South Bothnian boulder Bergsbrunna 1	
2	B 241	2.66	1.55	2.01	1.19	r	,,	Pl. IX, Figs. 2–3.
3	B 242	2.63	1.64	2.01	1.21	r	,,	Pl. IX, Figs. 5–7.
4	B 280	2.58	1.51	1.91	1.16	r	,,	
5	B 278	2.31	1.39	1.78	1.05	l	,,	
6	D 511	2.95	1.67	—	1.27	l	Siljan distr., Furudal	
7	D 430	2.85	1.57	2.24	1.25	r	,,	Pl. IX, Fig. 8.
8	D 510	1.68	0.95	—	—	l	,,	
9	D 431	2.87	1.67	2.23	1.34	l	Siljan distr., Fjäcka, loc. 3	Pl. IX, Fig. 1.
10	D 429	2.54	1.46	2.07	1.18	l	Siljan distr., Fjäcka, loc. 1	Pl. IX, Fig. 4.
11	Öl. 309	2.78	1.68	2.04	1.27	r	Öland, Böda Hamn bore, 6.24 m.	

Subvelar field narrow and of almost uniform width. Free margin with a row of coarse marginal tubercles.

Small instars of *T. dimorpha* differ from the larger specimens by more bulbous lobes and a much lower and comparatively broader velar ridge.

In all specimens examined L1, the connecting lobe between L1 and L3, and L3 are covered with rather large, closely spaced, deep pits. The pits extend through the greatest part of the thickness of the valve (Fig. 37), but according to the thin sections studied do not communicate with the interior of the valve. The lateral and ventral surface of the velar ridge is finely granulate.

Dimensions.—See Table 26.

Discussion.—The material studied shows a rather considerable variability in the length/height ratio of the valves, general outline, relative width of the lobes, and also in the extension of the anterodorsal end of the velar ridge. As this variability is observed also among specimens from the same locality and horizon it is obviously due to individual variation.

The specimens from Sweden seem to differ from those from the Uhaku Stage (C_1c) of Estonia described and figured by Öpik (1937) in the details of ornamentation. According to Öpik (1937, p. 24) the pits are confined in Estonian material to the ventral part of L1, whereas the Swedish specimens always possess pits also on L3. In other respects the Estonian and Swedish specimens are closely similar. Without an opportunity of examining material from the type locality it is difficult to form an opinion about the taxonomic value of this difference. If the difference in the ornamentation is constant a new subspecies must probably be erected for the Swedish specimens.

Occurrence.—In Estonia *T. dimorpha* has been found in the Uhaku Stage (C_1c) and, according to Sarv (1956a, p. 52), also in the Lasnamäe Stage (C_1b). The latter statement needs, however, further confirmation. In Sweden this species is common in the *Crassicauda* limestone, but occurs also in the lowermost part of the *Ludibundus* beds.

Estonia.—Tallinn; Uhaku; Purtse. *South Bothnian area.*—Erratic boulder Bergsbrunna no. 1 (10 specim.). *Siljan district.*—Vikarbyn (2 specim.); Fjäcka (11 specim.); Furudal, quarry at the rivulet Kalkbergsbäcken (9 specim.); Kårgärde (4 specim.). *Öland.*—Böda Hamn bore (6 specim.). *Västergötland*, Kinnekulle.—Kullatorp bore (4 specim.); Norra Skagen bore (17 specim., for the greatest part poorly preserved).

Tallinnella cf. *angustata* (Krause, 1891)

Pl. IX, Fig. 10.

cf. 1889 *Beyrichia marchica* n.sp.—Krause, pp. 19–20 (partim), Pl. II, Fig. 9.
cf. 1891 *Beyrichia marchica* var. *angustata* n.var.—Krause, p. 499.

The uppermost *Schroeteri* limestone of the Gammalsby bore yielded one left valve of a species of *Tallinnella* with general characters so similar to the specimen figured by Krause (1889, Pl. II, Fig. 9) and later (1891) named by him *Beyrichia marchica* var. *angustata* that it may well represent this species. However, on account of the rather bad preservation of the ornamentation of the specimen found, and of the too poor illustration by Krause their identity cannot at present be proved.

The specimen in question is on the whole rather similar to *Tallinnella dimorpha*, but differs by the following characters: (1) the dorsal part of L1 has a uniform width (long.), being parallel-sided and not bulbous as in *T. dimorpha*; (2) L2 is higher in dorsal view, and scarcely constricted ventrally; the summit of L2 lies at about the same level as that of L1; (3) L4 is generally higher, protruding in anterior view slightly more in lateral direction than the summit of the velar ridge; (4) the posterodorsal abrupt end of the velar ridge is situated at about the mid-height of the valve or only slightly dorsally from the latter. The ornamentation of the above specimen cannot be distinctly seen, but the ventral part of L1 seems to possess the same type of pits as *T. dimorpha*.

Dimensions of the specimen described.—Length of the valve 2.84 mm; height of the valve 1.68 mm; length of the lobate area 2.07 mm; height of the lobate area 1.26 mm.

Occurrence.—Uppermost *Schroeteri* limestone. Öland, Gammalsby bore, at the level of 6.30 m.

Tallinnella pachydactyla n. sp.

Pl. IX, Figs. 16–17.

Holotype.—Right valve (SGU), figured on Pl. IX, Figs. 16–17.

Type Locality.—Öland, Skärlöv bore.

Type Stratum.—Lowermost *Schroeteri* limestone, at the level of 3.35 m of the bore.

Derivation of the Name.—Greek παχύς = thick + δάκτυλος = finger, referring to the broad, finger-like lobes.

Diagnosis.—Lobes rather broad and swollen. L1 of more or less uniform width, L2 oblong, rather long (tr.), developed as a knob, separated from L1 by a furrow. Dorsal part of L3 bulbous, L4 broad and low. Extralobal area considerably narrower (tr.) than the velar ridge. Velar ridge low, rounded, in ventral view much lower than the lobes. Surface minutely granulate.

Description.—In all specimens found the posterior part of the valve is more or less fragmentary. L1 of more or less uniform width, rounded, sausage-shaped, highest point in anterior view almost at its dorsal end which tapers slightly, and protrudes beyond the dorsal margin of the valve in strictly lateral view. L2 developed as a knob, separated from the ventral part of L1 and the connecting lobe by a shallow furrow. The lobe has an oblong shape with posterodorsally directed axis, is rather long, with the highest point close to its dorsal end, slightly higher than the summit of L1 and slightly lower than that of L3. The connecting lobe between L1 and L3 of about the same width as L1, is rather low anteroventrally, and increases successively in height towards L3. L3 rather broad, slightly constricted in the middle, dorsal part expanded into an anteriorly directed bulb. Posterior margin of L3 almost straight in its dorsal part, dorsal end in strictly lateral view slightly protruding beyond the dorsal margin. Connecting lobe between L3 and L4 fairly low, expanding in posterodorsal direction into L4. The latter is low, broad, and possibly becomes obsolete before reaching the dorsal margin of the valve. It is broken off, or badly preserved, in all specimens examined. The details of its shape are therefore unknown. Extralobal area considerably narrower than the velar ridge, well defined but comparatively shallow.

Velar ridge low and broad, rounded posteriorly and posteroventrally, with a proximal keel anteroventrally and anteriorly; peripheral edge sharp. Anteriorly the ridge extends up to the anterior cardinal corner; position and shape of the posterior end not observed.

The ornamentation consists of a minute granulation on the lobes and a still more minute granulation on the lateral surface of the velar ridge.

Dimensions of the holotype.—Height of the valve 1.60 mm; height of the lobate area 1.30 mm.

Discussion.—*Tallinnella pachydactyla* n. sp. exhibits a rather close similarity to *T. trident* Henningsmoen. A new figure of the holotype of the latter species

is given on Pl. IX, Fig. 18. The main differences between these species are as follows: (1) L1 is in *T. pachydactyla* higher and more strongly curved posterolaterally; (2) L2 is larger and higher in this species; in *T. trident* the summit of L2 lies in anterior view considerably lower than that of other lobes; (3) L3 is broader in *T. pachydactyla*, and its dorsal part more strongly expanded; (4) the velar ridge is broader in lateral view in this species; (5) in *T. trident* L1 and L3 seem to protrude more beyond the dorsal margin of the valve; this is not visible on the photograph of the holotype (Pl. IX, Fig. 18), the dorsal portion of the valve being incomplete in this specimen. The details of the ornamentation are unknown in *T. trident*.

Occurrence.—*Tallinnella pachydactyla* n.sp. has been found only in the lowermost beds of the *Schroeteri* limestone. *Öland*, Skärlöv bore (3 specim.).

Tallinnella sebyensis n. sp.

Pl. IX, Figs. 12–13; Text-fig. 35B.

Holotype.—Left valve, UM no. Öl. 129, figured on Pl. IX, Figs. 12–13.

Type Locality.—Öland, Seby.

Type Stratum.—Gray *Schroeteri* limestone.

Diagnosis.—Lobes low and flattened. L1 broad, almost obsolete, merging anteriorly into the lateral surface of the velar flange; L2 rounded, separated from L1 by a shallow furrow, developed as a knob. In ventral view the summit of L3 lies at about the same level as that of L2. L3 well-defined, rounded, dorsal part slightly bulbous. L4 dorsally obsolete, or almost obsolete. Boundary between the lateral surface of the velar ridge and that of the domicilium formed ventrally by a distinct keel. Lateral surface of the velar structure flattened. Ventral part of L1 in one specimen with faint, small pits, ornamentation otherwise restricted to a faint reticulation.

Description.—L1 swollen, broad, flattened, curved posterodorsally, anterior and ventral boundaries poorly defined, dorsal boundary marked by a semisulcus. L2 developed as a fairly large, slightly oblong knob, separated from L1 by a shallow, poorly defined furrow. L3 rather broad, highest convexity close to its ventral end, dorsal part somewhat expanded, dorsal end not protruding beyond the dorsal margin of the valve. Connecting lobe between L3 and L4 narrow and low, slightly expanding in dorsal direction into a flattened, poorly defined L4. The latter becomes obsolete at about the mid-height of the valve. In dorsal or ventral view the summit of the ventral end of L3 lies at about the same level as that of L2.

Velar structure developed anteriorly and ventrally as a moderately broad, thick flange which is broadest anteriorly. The inner margin of the flange against the lateral surface of the domicilium is marked by a keel which becomes almost obsolete anteriorly. Posteriorly the keel merges into a broad, rounded

elevation. The lateral surface of the velar structure is gently sloping from the keel outwards; anteriorly where the keel is obsolete or almost so, this surface merges into L1 without any distinct boundary. Anteriorly the velar flange extends up to the anterior cardinal corner; posteriorly the velar flange ends rather abruptly slightly before reaching the posterior end of the valve. From this point the velar structure continues in dorsal direction as a low, broad elevation which runs more or less parallel to the posterior free edge of the valve almost up to the dorsal margin of the valve. In ventral view the velar flange is broadest and thinnest anteroventrally (cf. Pl. IX, Fig. 13). In posterior direction this flange becomes successively narrower (tr.) and at the same time thicker. It is thickest at its posterior end where the thickness of the velar flange as seen in ventral view is almost equal to its width (tr.) in lateral view at the same point. The subvelar field is moderately broad (tr.), widest at about the middle of the ventral margin, and decreases considerably in width in anterior direction until it ends at the cardinal corner very close to, or almost confluent with, the free edge.

The ornamentation consists of a faint reticulation, best visible on L1 and on the posterior third of the valve. The specimen from the Motala bore possesses also small, faint pits in the middle of the ventral part of L1. Extralobal area and lateral surface of the velar structure with a very fine concentrical striation. Most of this ornamentation is, however, so faint that it is scarcely visible on specimens with corroded surface.

Dimensions	Holotype	Right valve Motala 108.09 m
Length of the valve	2.71 mm	2.74 mm
Height of the valve	1.46 mm	1.42 mm

Discussion.—*Tallinnella sebyensis* resembles *T. tumida* some specimens of which are here figured for comparison (cf. Pl. IX, Figs. 14–15). It differs from the latter species, apart from the evidently much larger size, by the following main characters: (1) L2 is separated from L1 by a shallow and poorly defined furrow; (2) there is no keel on L2, whereas in *T. tumida* this is always present; (3) the velar structure is developed posteriorly as a broad, rounded ridge; (4) the lateral surface of the velar structure is convex ventrally, whereas in *T. tumida* this surface is ventrally more or less plane.

Tallinnella sebyensis differs from *T.* cf. *lata* mainly in the following respects: (1) the dorsal part of L4 is obsolete; (2) L3 is lower and more rounded; (3) the lateral surface of the velar structure is flattened; (4) the pits on the ventral part of L1 are, when present, considerably smaller and fainter.

Occurrence.—*Schroeteri* limestone. *Öland.*—Seby (1 specim.). *Östergötland.*—Motala bore (1 specim.).

Tallinnella cf. *lata* (Krause, 1891)

Pl. IX, Fig. 11.

cf. 1889 *Beyrichia marchica* n.sp.—Krause, p. 19 (partim).
cf. 1891 *Beyrichia marchica* var. *lata* n. v.—Krause, p. 499, Pl. XXXI, Figs. 14–15.

Description.—Only one valve known so far. L1 swollen, broad, dorsal part posterodorsally curved, anterior and ventral boundaries defined by a shallow furrow. L2 developed as a moderately large, slightly oblong knob, separated from L1 by a shallow furrow. L3 rather broad, its highest convexity close to its dorsal end, dorsal part expanded and forming a bulb which does not protrude beyond the dorsal margin of the valve. L4 low, rounded, dorsal end slightly expanded, reaching the dorsal margin, but not protruding beyond it. The dorsal end of L3 forms the highest point of the valve.

The velar structure forms a raised, rather thick ridge, in ventral view highest ventrally and considerably lower and less convex anteriorly. Posteriorly the velar ridge ends abruptly somewhat ventrally of the mid-height of the valve. In ventral view the summit of the ridge lies just in front of its posterior end. From the posterior end of the velar ridge a keel is running up to the hinge-line which it reaches a short distance anterolaterally from the posterior cardinal corner. Anteriorly the velar ridge extends up to the anterior cardinal corner. The extralobal area is developed as a furrow, strongest posteroventrally, and rather shallow and narrow anteriorly.

Ventral part of L1 with rather coarse, closely spaced, distinct pits of the same appearance as in *T. dimorpha*. A faint reticulation can be observed on the dorsal part of L1 and L4.

Dimensions.—Specimen RM no. Ar. 19811 (Pl. IX, Fig. 11): length of the valve 2.53 mm; height of the valve 1.35 mm.

Discussion.—The specimen described agrees in most of the important features with the figures of *T. lata* given by Krause (1891, Pl. XXXI, Figs. 14, 15). Krause does, however, not mention the pits on L1, L2 is drawn as if it were coalescent with L1 ventrally, and the dorsal end of L3 does not seem to be bulbous in his drawings. It is difficult to decide whether these differences are real or due to the inaccuracy of Krause's drawings. Full certainty in this question can be obtained only by a re-examination of Krause's original specimens.

For the distinguishing features between the specimen described and *T. sebyensis*, cf. p. 351. In some respects *T.* cf. *lata* resembles also *T. pachydactyla* n.sp. and *T. trident* Henningsm. However, in *T. pachydactyla* the ventral part of L1 is scarcely expanded at all, L2 is much larger, L3 is distinctly keeled along its posterior margin, the velar ridge is broader, and the extralobal area deeper and more distinct. Moreover, no pits have been observed on L1. *Tallinnella* cf. *lata* differs from *T. trident* by more rounded lobes, by the fact

that L4 extends up to the dorsal margin of the valve, and by a narrower extralobal area. In view of the above facts it is possible that the species determined here as *T.* cf. *lata* actually represents a new species, but additional material must be studied before its specific characters can be properly defined.

Occurrence.—Gray *Schroeteri* limestone. *Öland.*—Folkeslunda sjöbodar (1 specim.).

Gen. *Protallinnella* nov.

Type Species.—*Beyrichia grewingki* Bock, 1867.

Diagnosis.—Quadrilobate, L2 usually shorter than the other lobes. Velar flange frill-like, rather broad, broadest anteriorly, extending from one cardinal corner to the other and reaching the posterior cardinal corner close to the free edge. The flange is concave posteriorly and posteroventrally, but more or less convex anteriorly and anteroventrally. The subvelar field is high anteriorly and ventrally, but low posteriorly. A velar dimorphism may be present, but has not been ascertained so far.

Species.—Only the type species has been described. The present writer has had at his disposal material of two additional new species belonging to this genus, including one well-preserved, complete carapace (UM no. E 14).

Generic Characters.—Outline and lobation in general as in *Tallinnellina* n.gen. No dorsal plica has, however, been observed.

Velar structure developed as a rather broad flange extending from one cardinal corner to the other and reaching the posterior cardinal corner close to the free edge. The subvelar field is highest ventrally, and decreases gradually and conspicuously in height in posterodorsal direction becoming very narrow close to the posterior cardinal corner. Anteriorly the height of the subvelar field is only slightly less than ventrally; close to the anterior cardinal corner it diminishes rather rapidly the velar flange reaching the anterior cardinal corner close to the free edge. In all specimens examined by the present writer the velar flange is moderately concave posteriorly and posteroventrally, and more or less convex anteriorly and anteroventrally (cf. e.g. Öpik 1935, Pl. 2, Fig. 1a; Hessland 1949, Pl. IX, Figs. 3, 6a).

No dimorphism has so far been ascertained in *Protallinnella*, but is probably present (cf. also Henningsmoen 1954a, p. 49) as some specimens show a slightly broader and more convex velar flange anteriorly. The thin flange is, however, so easily broken off, especially anteriorly, that the material examined did not furnish conclusive evidence for the presence of a velar dimorphism.

The carapace in *Protallinnella* seems to be equivalved, with a marginal ridge or a marginal row of tubercles on either valve.

Discussion.—By the features of the velar flange *Protallinnella* can be clearly distinguished from other genera with a similar lobation, like *Tallinnellina* and *Tallinnella*. Morphologically it occupies a somewhat intermediate position

between these genera, but the exact relation cannot be stated until more material has been studied.

The North American *Tetradella subquadrans* Ulrich (1890, p. 115, Fig. 2) is on the whole rather similar to *Protallinnella*, except that the velar flange, according to the description by Ulrich, is concave in its whole extension, and that the subvelar field has a different shape anteriorly (cf. Ulrich 1890, p. 115, Fig. 2c). Without a first-hand knowledge of the American material the taxonomic position of this species cannot be settled at present.

Occurrence.—The genus *Protallinnella* n.gen. is known at present only from the *Expansus* and "*Raniceps*" limestones of Baltoscandia.

Gen. *Tallinnellina* nov.

Pl. X, Figs. 2, 4; Text-fig. 35C.

Type Species.—*Tetradella teres* Hessland, 1949.

Diagnosis.—Quadrilobate, L2 shorter than other lobes. Velar flange moderately broad, extending along the whole length of the free margin, concave in some specimens (tecnomorphs?), convex anteriorly and anteroventrally in others (heteromorphs?). Subvelar field high also posteriorly, the contact area between the velar ridge and the domicilium being placed rather high upon the side also at the posterior end of the valve. A faint dorsal plica at least in some species.

Species.— ? *Beyrichia erratica* Krause, 1889
Tetradella primaria Öpik, 1935
Tetradella lanceolata Hessland, 1949
Tetradella teres Hessland, 1949
? *Tetradella palmata* var. *valdaiensis* Neckaja, 1953
Tallinnellina n.sp. (figured as *Tetradella primaria* Öpik by Henningsmoen 1954a, Pl. 1, Fig. 4, refigured here on Pl. X, Fig. 2).

Generic Characters.—Domicilial outline slightly preplete, sometimes almost amplete. Dorsum of moderate height, more or less orthocline. Quadrilobate, lobes connected ventrally by a connecting lobe. L2 usually shorter than the other lobes and not reaching the dorsal margin. The other lobes extend to the dorsal margin, and may project beyond it. A faint dorsal plica is developed at least in some species.

The velar structure extends along the whole length of the free margin, developed as a moderately broad, frill-like flange which may decrease in width towards the posterior cardinal corner. The contact area between the velar structure and the domicilium lies posteriorly rather high up on the side, and

runs more or less parallel to the free edge. On the whole the subvelar field is, therefore, posteriorly as high as ventrally. If the velar flange is undamaged the position of the contact area in relation to the free margin can not often be clearly seen as the flange conceals the subvelar field. If, however, the flange is broken off, or posteriorly narrow, a ridge is formed which on the posterior part of the valve is situated as a rule closer to L4 than to the free edge. This is well illustrated in the specimen on Pl. X, Fig. 2. This course of the velar contact line has been observed by the present writer in *T. teres*, *T. lanceolata*, *T.* cf. *primaria* Öpik (from $B_{II}\beta$, Tallinn, Estonia, UM), *T.* n.sp. (Pl. X, Fig. 2), and also in *Rigidella*. The position of the velar structure on the posterior part of the valve of *Tallinnellina* differs clearly from that in *Protallinnella grewingki* (Bock). In the latter species the height of the subvelar field decreases considerably in posterodorsal direction, and the posterodorsal end of the velar flange is situated very close to the free edge and the posterior cardinal corner. This condition is the usual in *Eurychilinacea*.

Tallinnellina seems to possess a dimorphism very similar to that of *Rigidella*. The supposed dimorphic differences in the shape of the velar flange are at present best known in *T. teres*. In this species most of the valves possess a velar flange which along its whole extension is distinctly and rather strongly concave (cf. e.g. Hessland 1949, Pl. IX, Fig. 18a). In some large specimens the anterior and anteroventral part of the velar flange is, however, convex (cf. e.g. Hessland 1949, Pl. IX, Fig. 12; UM no. ar. os. 684). The course of the area of contact between the velar structure and the domicilium is evidently identical in specimens with an entirely concave as well as in those with a partly convex velar flange. These differences in the shape of the velar flange resemble those observed in *Rigidella*, and may be due to a velar dimorphism. Also the specimen of *Tallinnellina* n.sp. figured on Pl. X, Fig. 2, has a distinctly convex velar flange anteriorly and anteroventrally, and may represent a heteromorphic valve. More material should, however, be studied before the presence of a velar dimorphism in *Tallinnellina* can be said to be established with certainty.

Discussion.—The species included here in the genus *Tallinnellina* n.gen. obviously form a natural group which differs rather clearly from other related groups of species by the details of lobation and the features of the velar structure. *Tallinnella* is rather similar to *Rigidella*, and is certainly closely related to it. The main differences between them are found in the development of the posterior lobes. *Protallinnella* differs from *Tallinnellina* chiefly by the height of the subvelar field on the posterior part of the valve and by the shape of the velar flange in supposed tecnomorphs.

Occurrence.—Together with *Rigidella* *Tallinnellina* is one of the earliest eurychilinacean genera, appearing already in beds corresponding to the zone of *Megistaspis estonica* (*Tallinnellina* n.sp. from Heramb, Ringsaker, cf. Pl. X, Fig. 2). No Middle Ordovician species of this genus is known so far. Outside Baltoscandia the genus is unknown.

Gen. *Rigidella* Öpik, 1937

Pl. X, Fig. 5; Text-fig. 35D.

Type Species.—*Steusloffia mitis* Öpik, 1935.

Diagnosis.—L1 as a rule feebly developed, limited posteriorly by a very faint sulcus or a semisulcus, L2 prominent, shorter (tr.) than other lobes, constricted ventrally, L3 elongate, strongly convex, reaching almost to the dorsal margin, L4 flattened, delimited anteriorly by a semisulcus. The summits of all lobes are mostly provided with crests, united ventrally by a connecting crest. Velar flange moderately broad, entire, broadest anteroventrally, strongly decreasing in width posteriorly, concave in some specimens (tecnomorphs?), convex anteriorly and anteroventrally in others (heteromorphs?). A faint dorsal plica at least in some species.

Discussion.—Only the type species has been described so far. The present writer has examined 10 topotype valves of *Rigidella mitis*. In addition some valves of a new species of *Rigidella* have been at his disposal.

There has been some discussion about the real characters of the type species. Öpik (1935, p. 11, Fig. 4) gives a diagrammatic drawing of the holotype, but the correctness of this drawing was strongly questioned by Henningsmoen (1953a, pp. 221–223, Fig. 19) who gives a new diagrammatic reconstruction of the holotype (Henningsmoen 1953a, Fig. 10c) based on a study of the photograph published by Öpik (1935, Pl. 1, Fig. 5). The genus was characterized by Öpik (1937, p. 53) as trilobate. Hessland (1949, p. 339) considered the type species of *Rigidella* to be quadrilobate. Henningsmoen (1953a, pp. 222–223) states that *Rigidella mitis* has four lobes, but that L3 and L4 are separated by a semisulcus only and that *Rigidella* thus possesses only two real sulci. According to him the crests in this genus form a normal "tetradellide" pattern, and the hindmost ridge on Öpik's figure obviously belongs to the velar structure.

The examination of *Rigidella mitis* by the present writer has confirmed Henningsmoen's conclusions. This species seems, however, to possess only one sulcus, as the furrow between L2 and C1 does not seem to leave any clear trace interiorly, and is thus obviously an ornamental structure, exactly as in *Steusloffia*. On some specimens, however, a slight trace of a sulcus between L1 and L2 is visible on the internal mould. S1 may thus be developed as a semisulcus or as a very faint sulcus. L3 is delimited posteriorly by a semisulcus. Öpik's drawing is not quite correct. The posterior ridge in his drawing belongs to the velar flange which is broken off, and represents in reality the contact line between the velar structure and the domicilium. There is no connection between this ridge and the crests. All lobes bear on their summit a distinct crest, that of L2 and L3, however, being missing on young instars. A low dorsal plica is present at least in large specimens. The ornamentation is reticulate, resembling that of *Tallinnellina lanceolata*. The velar flange is

usually concave and broadest anteroventrally. In posterior direction the width of the flange decreases considerably, and near the dorsal margin of the valve the velar structure seems to change into a ridge. The contact area between the velar structure and the domicilium is placed rather high upon the side posteriorly, and there runs more or less parallel to the free edge. The subvelar field is, therefore, rather high even posteriorly as in *Tallinnellina*. In some specimens the anteroventral part of the velar flange is slightly convex and a little broader than the corresponding part of the velar structure in valves with a concave flange (cf. Pl. X, Fig. 5). These specimens may represent heteromorphs, and thus *Rigidella* may possess a velar dimorphism of the same character as that of *Tallinnellina*. The ends of the probable dolon are rather indistinct, the convex part of the velar flange changing smoothly into the common concave type exhibited, *inter alia*, by all small valves of *Rigidella mitis*.

Rigidella bears on the whole a considerable likeness to *Steusloffia*, possessing the same general lobation and a similar type of arrangement of the crests. It differs from *Steusloffia* mainly by: (1) L3 being long and reaching the dorsal margin and, therefore, not being developed as a posteroventral lobe, and (2) the obvious presence of a velar dimorphism, not known in *Steusloffia*. *Tallinnellina* is, however, even more similar being evidently dimorphic, and possessing amongst others an identical course of the posterior part of the contact area between the velar structure and the domicilium. From this genus *Rigidella* differs almost only by the obsolescence of S1 and S3. Obsolescence of S1 occurs also within other genera (as in *Tallinnella*) and is probably not of generic value. Moreover, a faint trace of it may be recognized even in *Rigidella*. The obsolescence of S3, however, seems to be of greater importance. There is no doubt that *Rigidella* and *Tallinnellina* are closely related and if intermediate forms are found these genera should probably be regarded as subgenera of a single genus.

As pointed out by Hessland (1949) and Henningsmoen (1953a) *Steusloffia* evidently has developed from forms similar to *Rigidella* and *Tallinnellina*. In this case the evolution may comprise also loss of ability to produce a velar dimorphism. In the present writer's opinion the morphological series illustrated by Henningsmoen (1953, p. 220, Fig. 9) gives a correct idea of the main course of the evolution in *Rigidella* and *Steusloffia*.

Öpik (1937, p. 53) included a number of species in his genus *Rigidella*. Hessland (1949, pp. 338–340), on the other hand, considered most of them to belong to *Steusloffia*, and restricted the genus *Rigidella* to the type species. *Beyrichia erratica* Krause, 1889, was considered by him to belong to *Tetradella* (= *Tallinnellina*). The figure of the lectotype (designated by Öpik 1935, p. 11) of *Beyrichia erratica* (Krause 1889, Pl. II, Fig. 7) shows a distinctly quadrilobate valve which is very similar to *Tallinnellina*, and this species may well belong to the latter genus. But this figure, like most figures by Krause,

may be incorrect in its details. Later HENNINGSMOEN (1953a, Pl. 1, Figs. 3, 4 and 1954a, Pl. 1, Figs. 2, 3) figured a specimen from an erratic boulder at Kristdala, Småland, as *Rigidella erratica*. After an examination of this specimen the present writer considers it, however, as belonging to *Steusloffia*. In this specimen the arrangement of the crests is similar to *Rigidella* (as is the case also with other early *Steusloffia* species), but L3 is restricted to the ventral part only, thus forming a posteroventral lobe, characteristic of *Steusloffia*. As long as only one specimen is known nothing can be said about the possible dimorphism. The specimen figured by HENNINGSMOEN may belong to *Steusloffia krauseana* (E. A. SCHMIDT, 1941) (= *Beyrichia erratica* in KRAUSE 1889, Pl. II, Fig. 8), but KRAUSE's figure is too poor for the establishment of the identity with any reasonable degree of certainty.

The specimens from the *Megalaspis* limestone (3cα) of Slemmestad, Røyken, Oslo region, placed by HENNINGSMOEN (1954a) into *Rigidella erratica* and examined by the present writer, undoubtedly belong to *Rigidella*. They very much resemble the type species, but their rather bad state of preservation prevents at present a safe specific determination. Until further notice they may be regarded as *Rigidella* cf. *mitis* (ÖPIK). The other species referred by ÖPIK (1937, p. 53) to *Rigidella* belong, as pointed out already by HESSLAND (1949, p. 354), to *Steusloffia* or are so far generically indeterminable.

OCCURRENCE.—*Rigidella* is one of the earliest eurychilinacean genera known. A new species of this genus has been found in limestone boulders at Örebro, belonging probably to the zone of *Megistaspis estonica* of the Billingen Stage (Arenig) (TJERNVIK 1956, p. 163). The type species comes from the *Lepidurus* limestone, and similar specimens have been found in the approximately contemporaneous *Megalaspis* limestone (3cα) of the Oslo region. At present the genus is unknown outside Baltoscandia.

Gen. *Steusloffia* ULRICH & BASSLER, 1908

TYPE SPECIES.—*Strepula Linnarssoni* KRAUSE, 1889 (subsequent designation by ULRICH & BASSLER 1923a, p. 308).

DIAGNOSIS.—Unisulcate, with a long and broad sulcus, a large presulcal knob (L2), and a distinct posteroventral lobe (= ventral part of L3). Adult valves with four crests: C1 in front of the presulcal knob, C2 upon the presulcal knob, C3 upon the posteroventral lobe, and C4 behind the posteroventral lobe. Ventral ends of C1, C3, and C4, and in some species also that of C2, united ventrally. A dorsal ridge is as a rule developed. Velar structure moderately broad, plane to concave, flange-like, becoming ridge-like or obsolete before reaching the posterior cardinal corner. No dimorphism known.

SPECIES.—*Beyrichia costata* LINNARSSON, 1869
Strepula linnarssoni KRAUSE, 1889

Beyrichia erratica var. *acuta* KRAUSE, 1891
Strepula simplex KRAUSE, 1891 (probably erected on a young instar)
Strepula lineata var. *granulosa* STEUSLOFF, 1894
Strepula lineata var. *separata* STEUSLOFF, 1894
Steusloffia multimarginata ÖPIK, 1937
Steusloffia rigida ÖPIK, 1937
Steusloffia humilis ÖPIK, 1937 (probably erected on a young instar)
Rigidella krauseana E. A. SCHMIDT, 1941
Steusloffia polynodulifera HESSLAND, 1949

Strepula lineata var. *granulosa* and *S. lineata* var. *separata* were regarded as subjective synonyms by KUMMEROW (1924, p. 408) who based himself upon an examination of the type material of STEUSLOFF (1894). HENNINGSMOEN (1954a, p. 53) considered these two forms and *Steusloffia polynodulifera* to be subjective synonyms of *S. acuta* (KRAUSE). It seems to be very difficult at present to take up a definite attitude as to the synonymy of these forms. The descriptions of KRAUSE (1889) and STEUSLOFF (1894) are incomplete, and their figures may not be correct in minor but taxonomically important details. It seems probable that HENNINGSMOEN is right in regarding all of them as synonyms. Further studies on Baltoscandian Lower Ordovician species of *Steusloffia* are, however, needed in order to settle this question definitely. The arrangement of the crests on the specimen figured by KRAUSE as *Strepula simplex* strongly resembles that in young instars of other species of *Steusloffia*, and this species may therefore have been erected on a young instar.

Even on the Middle Ordovician species of the genus *Steusloffia* opinions have been widely divergent. ÖPIK (1937), attributing in defining the species a considerable diagnostic value to the arrangement of the crests, distinguished 4 species. KUMMEROW (1939, pp. 91–96) rather severely criticized ÖPIK's conception of the species of *Steusloffia*, and was joined therein also by E. A. SCHMIDT (1941, p. 51). According to KUMMEROW the interspecific variation of the arrangement of the crests is so considerable that only one highly variable species *S. linnarssoni* can be distinguished, all other species described by ÖPIK (1937) being subjective synonyms to it. KUMMEROW also described for the first time changes of the crests during the ontogenetic development, and pointed out that *S. humilis* ÖPIK has been erected on a young instar. THORSLUND (1940, pp. 176–178), without knowing KUMMEROW's paper, arrived on the whole at the same conclusion as KUMMEROW (1939), and regarded *S. costata*, *S. linnarssoni*, and with some doubt also *S. multimarginata* as belonging to one species called after the oldest name *S. costata* (LINNARSSON). He, thus, also changed the name of the type species of *Steusloffia*. He likewise described changes of the crests during the ontogenetic development. Later, however, THORSLUND (1948) became aware that in the Middle Ordovician of Sweden

at least two different species of *Steusloffia* could be distinguished which he called *S. costata* and, provisionally, *S.* aff. *costata*.

During the preparation of the present paper it soon became apparent that the arrangement of the crests in *Steusloffia* is much stabler than assumed by Kummerow and Thorslund (1940). The rather extensive material of *Steusloffia* from the *Schroeteri* and *Crassicauda* beds of the bores of Gammalsby and Norra Skagen show one rather constant type of the arrangement of the crests, the finely preserved material from the boulders of Tvären a second, and the specimens from the upper part of the *Ludibundus* beds of the Kullatorp core a third type. These three types of arrangement of the crests of *Steusloffia* characterize on the whole different stratigraphic horizons, and all the material from each horizon is in this respect remarkably uniform. In addition to the characters of the crests there exist other equally constant differences especially in the shape of the posterior part of the velar flange. Further material from other bores and localities has fully confirmed the first observations. Kummerow's (1939) material from the drift boulders evidently forms a mixture from different stratigraphic horizons, and his criticism of Öpik's (1937) conception of the species of *Steusloffia* is quite unwarranted except for the point that *S. humilis* Öpik is erected on a young instar.

The material studied contains three distinctly different species of *Steusloffia*. The specimens from the *Schroeteri* and *Crassicauda* beds are obviously conspecific with *Strepula linnarssoni* Krause, 1889, and thus represent the type species. The specimens from the lower part of the *Ludibundus* beds including the material from the Tvären boulders are, as pointed out already by Thorslund (1940, p. 178), very similar to *S. multimarginata* Öpik, and the present writer considers them as conspecific. The species from the middle and upper part of the *Ludibundus* beds represent the real *S. costata* (Linnarsson).

Strepula lineata Krause, 1889, was included in *Steusloffia* by Bassler & Kellett (1934, p. 475), and with some doubt also by Hessland (1949, p. 339). Without having studied the original material it is difficult to ascertain the taxonomic position of this species, but as no posteroventral lobe seems to be developed, this species hardly belongs to *Steusloffia*.

Generic Characters.—*Steusloffia* should obviously be regarded as an unisulcate genus, the sulcus being formed by S2. Although a fairly shallow and narrow furrow, corresponding according to Hessland (1949, p. 352) to S1, is formed between C1 and the presulcal knob, no distinct impression of it on internal moulds has been observed by the present writer. Thus this furrow evidently is an ornamental feature. S2 is long and broad, expanding dorsally and narrowing in the ventral direction. On internal moulds the ventral delimination of the sulcus is fairly indistinct, the furrow becoming increasingly shallower, and merging gradually into the general surface of the ventral part of the valve. The ventral end of the sulcus is as a rule slightly curved anteroventrally.

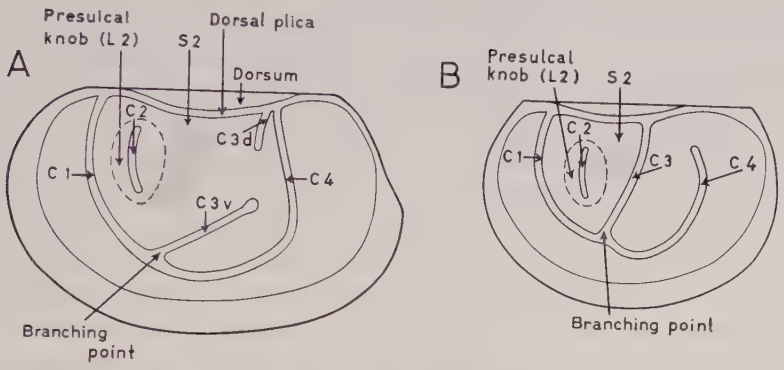


Fig. 38. Explanation of some terms of the valve of *Steusloffia*. A, a valve of *Steusloffia* of the Middle Ordovician type; B, a valve of *Steusloffia* of the Lower Ordovician type. Further explanation in the text.

In all species of *Steusloffia* the ventral part of the postadductorial area is characteristically inflated, forming a posteroventral lobe. This lobe corresponds to the ventral part of L3 as can be distinctly seen on comparing *Steusloffia* with *Rigidella*. Upon the internal moulds the lobe is usually well defined anteriorly and dorsally, but more or less indistinctly ventrally and posteriorly. A rounded or transversally oblong, rather large knob in front of the sulcus corresponds to L2 (cf. Hessland 1949, p. 353). Upon internal moulds the anterior limit of the knob is usually formed by a rather abrupt change in convexity which can be called a semiculcus.

Steusloffia can be said to be indistinctly quadrilobate. The areas of the lateral surface of the domicilium in front of L2 and behind L3 correspond to L1 and L4, respectively, L2 being developed as a knob, and L3 as a posteroventral lobe. This interpretation is confirmed by comparison of *Steusloffia* with *Rigidella* (cf. also Henningsmoen 1953a, p. 220, Fig. 9). A rather similar type of lobation occurs also in some species of *Tallinnella* as for instance in *Tallinnella tumida* (Pl. IX, Figs. 14–15) and *Tallinnella sebyensis* (cf. Pl. IX, Fig. 12) except that in these species L3 reaches the dorsal margin.

The lateral surface of the domicilium is characteristically ornamented with crests. In late instars and adult valves four crests are almost invariably present, and wholly or partly connected ventrally. The terms proposed by Hessland (1949, p. 129, Fig. 3c) for these crests are adopted here, but following Kesling (1951c) and Henningsmoen (1953a) the numbers of the crests are given in Arabic instead of Roman figures. Hessland's terminology of the crests is superior to that of Öpik (1937, pp. 50–51, Figs. 7 and 9) by conveying an idea of their comparative morphological relations, and also by being shorter. The crests are thus termed C1, C2, C3, and C4 (Fig. 38), and a comparison with *Rigidella* distinctly shows that they have originally been linked to the lobes L1, L2, L3, and L4, respectively (cf. Hessland 1949, p. 353; Henningsmoen

1953a, p. 220, Fig. 9). With regard to the arrangement of the crests two distinct groups of species can be distinguished in *Steusloffia*. In the Lower Ordovician species, as in *S. acuta* and allied species (cf. KRAUSE 1891, Pl. XXXI, Fig. 18; STEUSLOFF 1894, Pl. LVIII, Figs. 22, 23a; HESSLAND 1949, Pl. X, Figs. 2a, 3, 7; HENNINGSMOEN 1953a, p. 220, Fig. 9c, Pl. 1, Figs. 3, 4; 1954a, Pl. 1, Figs. 2, 3), C3 is uninterrupted, running continuously from the branching point (see Fig. 38 B) up to the dorsal plica. In the Middle Ordovician species, like those described in the present paper and *S. rigida* ÖPIK (1937, p. 51, Fig. 8, Pl. IV, Figs. 1, 2), C3 is interrupted in the middle, the ventral branch usually reaching the top of the posteroventral lobe in order to terminate there in a little node, and the dorsal branch beginning below the lobe. These separate branches of C3 are termed here C3 v (= ventral branch), and C3 d (= dorsal branch) (cf. Fig. 38 A). C1, C3, and C4 are as a rule united ventrally. Their point of junction is regarded here as the ventral end of the respective crests, and is called the branching point. If the species are arranged according to their stratigraphic occurrence the branching point tends to assume an increasingly anterior position as pointed out by HENNINGSMOEN (1953a, p. 223). This trend is well illustrated by HENNINGSMOEN (1953a, p. 220, Fig. 9), and further confirmed by the material studied by the present writer. The stratigraphically oldest species studied here, *S. linnarssoni*, exhibits the most posterior position of the branching point; *S. multimarginata* is intermediate in the position of the branching point as well as stratigraphically, and in the stratigraphically youngest species, *S. costata*, the branching point lies far anteriorly (cf. Fig. 40). This morphological series may, however, not correspond to the real evolutional lineage in *Steusloffia* since *S. rigida*, contemporaneous with *S. linnarssoni*, shows a position of the branching point intermediate between *S. multimarginata* and *S. costata*.

Changes in the crests during the ontogenetic development have been described by KUMMEROW (1939, p. 95, Figs. 18, 19) and THORSLUND (1940, p. 177, Fig. 58, Pl. 3, Figs. 2–4 = *S. multimarginata*). They have been studied also by the present writer in *S. multimarginata* and *S. costata*. Generally, in the species studied so far in early instars, C1 and C3 appear first, and C4 last. THORSLUND (1940, p. 177) expressed the opinion that the crest and the dorsal ridge seem to be due at least to some extent to a confluence of tubercles. The material studied by the present writer is, however, not univocal in this respect, the tubercles and the position of the crest exhibiting on most specimens no distinct correspondance (cf. also Pl. X, Figs. 13, 14).

In all species of *Steusloffia* a dorsal plica is obviously present, but is rather easily broken off as pointed out by KUMMEROW (1939, p. 94). Thus in the specimen figured by KRAUSE (1889, Pl. II, Fig. 4 = *S.* cf. *multimarginata*), and refigured diagrammatically by ÖPIK (1937, p. 50, Fig. 7) and KUMMEROW (1939, p. 92, Fig. 14) the dorsal plica is certainly broken off. Posteriorly the dorsal plica coalesces with the velar structure. Dorsally of the sulcus the plica

runs in a wide, ventrally directed curve, thus leaving a rather broad space between the dorsal plica and the dorsal margin (cf. also KUMMEROW 1939, p. 94). In most species the dorsal plica is developed as a crest similar to other crests of the valve. It may also be broader, and protrude beyond the dorsal margin as especially in *S. costata* (cf. Fig. 40 A). The dorsum is usually rather high anteriorly and posteriorly, and continuous with the outer side of the dorsal plica, but is mostly hypocline in the middle, between the ventrally directed curve of the plica and the dorsal margin.

The velar structure is developed as a moderately broad, concave flange or frill which is non-undulate or very slightly undulate. The anterodorsal end of the velar structure is confluent with the dorsal plica. Posterodorsally the velar flange usually becomes obsolete before reaching the posterior cardinal corner, continuing in dorsal direction as a more or less distinct ridge which is confluent with the dorsal plica. The degree of posterior restriction of the velar flange forms in the species studied a morphological series which on the whole conforms to that of the position of the branching point of the crests, the posterior end of the velar flange assuming a more ventral position in stratigraphically younger species. In *S. linnarssoni* the posterior end of the velar flange reaches highest dorsally, *S. multimarginata* is intermediate even in this respect, and in *S. costata* the velar flange ends abruptly rather far ventrally (cf. Fig. 40). Also from this point of view *S. rigida* is rather advanced in spite of being relatively old stratigraphically, the posterior termination of the velar flange being similar to that in *S. costata*, if we may judge from the figure given by ÖPIK 1937 (Pl. IV, Fig. 2). In the Lower Ordovician *S. polynodulifera* the velar structure resembles that of *S. linnarssoni* (cf. HESSLAND 1949, Pl. X, Fig. 2a, b). As the velar structure is confluent with the dorsal plica at either end of the valve, the former runs dorsally at some distance from the free margin and the cardinal corners, the contact area between the velar structure and the domicilium being in end views more or less parallel to the free margin. In the specimens described by HENNINGSMOEN (1953a, Pl. 1, Figs. 3, 4) as *Rigidella* cf. *mitis* and, later (1954a, Pl. 1, Figs. 2, 3), as *Rigidella erratica* (= *Steusloffia* cf. *krauseana*) the contact area between the velar structure and the domicilium is placed posteriorly rather high up the side of the valve, reminding much of that in *Rigidella*. In most other species the subvelar field is posteriorly lower.

As observed already by ÖPIK (1937, Pl. XII, Fig. 9; TRIEBEL 1941, Pl. 6, Fig. 61) the peripheral margin of the velar flange appears to be double in ventral view. The material studied by the present writer shows that both simple and double peripheral ventral margins of the velar flange occur in all species described here. The simple type of the ventral margin of the velar flange is figured on Pl. X, Fig. 16. In other specimens the peripheral margin is ventrally double (cf. Pl. XI, Fig. 1), a distinct furrow separating an outer and an inner edge (cf. Fig. 39). The outer (lateral) edge evidently corresponds to

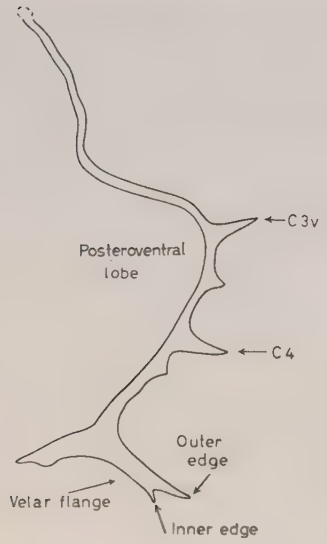


Fig. 39. *Steusloffia multimarginata* Öpik. Diagrammatic drawing of a transversal section of a valve with double ventral margin of the velar frill. After a thin section of a specimen from the Tvären area. × 30.

the peripheral edge of the specimens with the simple type of velar flange. The inner edge exists only ventrally, and merging into the general inner surface of the velum disappears rather abruptly in posteroventral and anteroventral direction. In lateral view the outer edge protrudes more in ventral direction concealing the inner edge and for this reason it is rather difficult in specimens embedded in the rock to expose the inner edge without breaking the rather thin velum. No difference in appearance of the lateral side of the valve seems, for the time being, permit a distinction between the specimens with simple and with double ventral margin of the velum. Thus the examination of the inner side of the velum is the only reliable way of distinguishing between them. In some rare cases immersion of the specimen in alcohol or oil has revealed the inner edge as a dark line. From among the large number of specimens of *Steusloffia* studied, however, the development of the ventral margin could be ascertained only in a few pieces. The size distribution of these two types of velum is, therefore, as yet incompletely known. All specimens in which the simple ventral margin of the velum could be observed are young instars with incompletely developed crests. In the larger specimens on which the inner side of the velar flange was exhibited the velum had a double ventral margin. The size distribution of these specimens suggests that this character occurs not only in the adult specimens, but also in late instars with completely developed crests. Thus the double ventral margin of the velum is probably not a dimorphic character, as the present writer was at first inclined to believe, but a character acquired at some late stage of the ontogenetic development. At present the double ventral margin of the velum is known in *Steusloffia* only in the Middle Ordovician species (*S. rigida*, *S. linnarssoni*, *S. multimarginata*, *S. costata*), and

no information exists about the structure of the inner side of the velar flange in the species from the Lower Ordovician.

The subvelar field in *Steusloffia* is as a rule slightly concave, and quite close to the free edge a marginal ridge is developed which usually bears a row of spines. These spines are visible in lateral view of undamaged valves dorsally from the posterior end of the velar flange where the free edge forms a part of the lateral outline of the valve.

Discussion.—As pointed out especially by Henningsmoen (1953a) *Steusloffia* certainly is derived from *Rigidella*-like ancestors. There has been much discussion about the boundary between these genera (Öpik 1937, p. 53; E. A. Schmidt 1941, pp. 39–40; Hessland 1949, pp. 339–340; Henningsmoen 1953a, pp. 221–224; 1954a, p. 52; cf. also in the present paper p. 357). After having studied new material of the type species of *Rigidella* the present writer considers as belonging to *Steusloffia* forms in which L3 is developed as a posteroventral lobe, and in which no velar dimorphism is present. For further discussion about the relations between these genera, see p. 357.

Pseudostrepula is a genus externally resembling *Steusloffia*. It has the same kind of presulcal knob, generally smaller than in *Steusloffia*, and the same general characters of arrangement of the crests which are, however, bifurcated dorsally. Also the velar structure is developed similarly to *Steusloffia*, and in spite of the examination of numerous specimens no velar dimorphism is known at present. As pointed out by Henningsmoen (1953a, p. 215) the specimen of *Pseudostrepula kuckersiana acuta* figured by Bonnema (1909) on Pl. VI, Fig. 26 shows a faint undulation on the anteroventral part of the valve, but the real character of the undulation is unknown at present. No specimens with such undulation have been observed in this species by the present writer. *Pseudostrepula* differs from *Steusloffia*, especially by having no posteroventral lobe, by the dorsal bifurcation of the crests, and by a relatively smaller presulcal knob. These genera may be related, but the proximity of their relation is unknown at present.

Kummerow (1924, p. 406) reported that his examination of the type specimen of *Entomis umbonata* Steusloff, 1894, has proved this to be a specifically indeterminable internal mould. As pointed out by Henningsmoen (1953a, pp. 224–225) it very much resembles the internal moulds of *Steusloffia*, and the present writer is inclined to agree with him. But the exact taxonomical position of that species can probably never be ascertained. *Entomis umbonata* was made the type species of the genus *Ctenentoma* by E. A. Schmidt (1941). This genus is thus erected on a nomen dubium (declared as such already by Kummerow 1924), and must itself be regarded a nomen dubium. It may be a junior subjective synonym to *Steusloffia* as suggested by Henningsmoen (1953a, p. 225), but this cannot be proved with any reasonable degree of certainty. For this reason also the subfamily *Ctenentominae* E. A. Schmidt, 1941, must be regarded a nomen dubium.

Occurrence.—The earliest known species of *Steusloffia* comes from the *Expansus* limestone (Upper Arenig) of Sweden, and specimens of the genus have been found up to the *Macrourus* beds of Sweden. Outside Baltoscandia no species referable with certainty to *Steusloffia* is known at present.

Steusloffia linnarssoni (Krause, 1889)

Pl. X, Figs. 6–10; Text-fig. 40B.

1889 *Strepula linnarssoni* n.sp.—Krause, p. 16, Pl. II, Fig. 5 (non Pl. II, Fig. 4 = ? *Steusloffia multimarginata* Öpik, 1937).

1908 *Beyrichia* (*Steusloffia*) *linnarssoni* (Krause)—Ulrich & Bassler, p. 296, Fig. 34, Pl. XXXVIII, Fig. 1 (copies from Krause 1889, Pl. II, Fig. 5) (non p. 282, Text-fig. 8, copied from Krause 1889, Pl. II, Fig. 4 = ? *Steusloffia multimarginata* Öpik, 1937).

1923a *Steusloffia linnarssoni* (Krause)—Ulrich & Bassler, p. 306, Fig. 18: 5 (after Krause 1889, Pl. II, Fig. 5), p. 308.

? *1924* *Steusloffia Linnarssoni* Krause sp.—Kummerow, p. 441.

1934 *Steusloffia linnarssoni* (Krause)—Bassler & Kellett, p. 24, Fig. 9: 5 (copied from Ulrich & Bassler 1923a, Fig. 18: 5 after Krause 1889, Pl. II, Fig. 5), p. 475.

1940 *Steusloffia costata* (Linnarsson)—Thorslund, p. 176 (partim).

1948 *Steusloffia* aff. *costata* (Linnarsson)—Thorslund, pp. 344, 360, 369 (partim).

1953b *Steusloffia costata* (Linnarsson)—Henningsmoen, p. 44.

non 1937 *Steusloffia linnarssoni* (Krause)—Öpik, p. 50, Text-fig. 7 (diagram after Krause 1889, Pl. II, Fig. 4), p. 51 = ? *Steusloffia multimarginata* Öpik, 1937.

non 1939 *Steusloffia linnarssoni* (Krause)—Kummerow, p. 92, Fig. 14 (copy of the diagram in Öpik 1937, Text-fig. 7 = ? *Steusloffia multimarginata* Öpik, 1937).

Lectotype.—Right valve figured by Krause 1889, Pl. II, Fig. 5 (designated herein). Öpik (1937, p. 50, explanation of the Text-fig. 7) has called the specimen figured by Krause 1889, Pl. II, Fig. 4, "type specimen", but as far as the present writer can understand the term "type specimen" is used in the sense of "cotype", and no actual designation of the lectotype has taken place. It would be unfortunate to regard that specimen as the lectotype as its specific characters can not be properly understood at present. It is probably not conspecific with the specimen on Pl. II, Fig. 5 in Krause 1889 here designated as the lectotype which represents the type usually determined as *S. linnarssoni*. The lectotype is apparently lost, and a neotype must therefore be determined.

No Type Locality, since the lectotype was found in a glacial drift boulder.

Exact Type Stratum unknown (probably from *Schroeteri* or *Crassicauda* limestone).

Diagnosis.—The branching point of the crests lies slightly behind or at the transversal line through the middle of the presulcal knob. C3v and C4 diverge

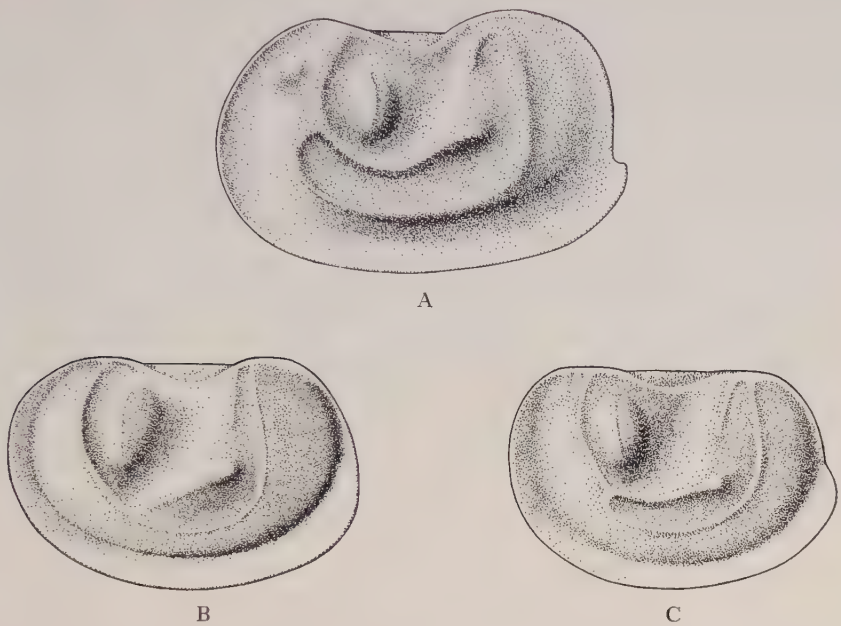


Fig. 40. Reconstruction of (A) *Steusloffia costata* (Linnars.), (B) *S. linnarssoni* (Krause), and (C) *S. multimarginata* Öpik. A, after the specimen figured on Pl. X, Fig. 18; B, after that on Pl. X, Fig. 6; and C, after that on Pl. X, Fig. 11. The marginal spines and the ornamentation are omitted. × 35.

strongly behind the branching point. C3 divided into a dorsal and a ventral branch. The velar flange changes into a ridge posteriorly at about the longitudinal line through the middle of the presulcal knob.

Description.—Posteroventral lobe transversally rather long, its top forming the highest part of the valve (Pl. X, Fig. 9).

C3v directed posterodorsally, more or less straight (Pl. X, Fig. 6), or slightly curved (Pl. X, Figs. 7–8, 10), terminating in a little node on the top of the posteroventral lobe. Branching point of the crests slightly behind or at the transversal line through the middle of the presulcal knob. Behind this point C3v and C4 diverge rather strongly. C3v always present, ventral end usually reaching the dorsal end of the posteroventral lobe, but sometimes also slightly shorter. C2 confined to the presulcal knob. Dorsal plica scarcely broader or higher than the crests, anteriorly and posteriorly continuous with the velar structure. In strictly lateral view the dorsal plica protrudes anterodorsally and posterodorsally slightly beyond the hinge-line.

In anterodorsal direction the velar flange decreases gradually in width up to the point of coalescence with the dorsal plica. Posterodorsally the velar flange decreases more or less evenly in width, and at about the longitudinal line through the middle of the presulcal knob changes into a distinct velar ridge which continues dorsally up to the coalescence with the dorsal plica.

Table 27.

No.	Mus. cat. no.	H. valve	L. domic.	H. domic.	H-L	Valve	Locality	Remarks
1	SGU	1.51	2.10	1.28	—	l	Gammalsby 8.20 m	Figured on Pl. X, Fig. 6.
2	,,	—	2.09	1.28	—	l	Gammalsby 0.60 m	Figured on Pl. X, Fig. 10.
3	,,	—	1.42	0.88	—	r	Gammalsby 0.35 m	
4	UM B 302	—	1.94	1.19	1.40	l	Erken 10	Figured on Pl. X, Figs. 8–9.
5	SGU	1.30	1.71	1.14	—	r	Motala 108.83 m	
6	,,	—	1.95	1.25	—	r	Smedsby Gård 117.12 m	
7	,,	—	1.67	1.10	—	r	Smedsby Gård 115.93 m	
8	,,	—	2.12	1.28	—	l	Norra Skagen 23.39m	Figured on Pl. X, Fig. 7.
9	,,	1.31	1.79	1.13	—	l	Norra Skagen 22.93 m	
10	,,	—	2.23	1.36	—	l	Stora Åsbotorp 63.54 m	

No such abrupt change in the width of the velar structure at the posterior end of the valve as in *S. multimarginata* or *S. costata* has been observed.

Ornamentation on the whole as in *S. multimarginata*.

Dimensions.—See Table 27. In spite of a great number of specimens examined of this species few specimens were sufficiently well preserved for measuring. This is due mainly to the fact that most specimens occur in argillaceous or finely nodular limestones, where they are often badly preserved. When measuring the height of the valve or of the lateral surface of the domicilium the dorsal end of the dorsal plica was regarded as the dorsal boundary in this species as well as in other species of *Steusloffia* described.

Discussion.—Although fairly numerous specimens of this species have been obtained, only few had a more or less complete velum. In order to define the degree of variation of the velar characters in this species more and better preserved material is needed. The possibility of the specimens determined here as *S. linnarssoni* representing more than one species is still not quite excluded.

In general *S. linnarssoni* is rather similar to *S. multimarginata*. It obviously reaches not such a large size as the latter species (the largest specimen examined has a length of the lateral surface of the domicilium of 2.25 mm). Instars equalling in size those of *S. multimarginata* with incompletely developed crests have in *S. linnarssoni* a development of the crests essentially similar to that of adult valves. The most conspicuous difference between *S. linnarssoni* and *S. multimarginata* lies in the direction of C3v. In the former species this is always strongly posterodorsally directed, and behind the branching point

C3v and C4 diverge rather strongly. In *S. multimarginata* C3v is almost exactly posteriorly or slightly posterodorsally directed, and more or less parallel to C4. Moreover, in this species the posterior change from the velar flange to a velar ridge is rather abrupt, and takes place at about the longitudinal line through the branching point of the crests, or slightly more ventrally. In *S. linnarssoni* no such abrupt ending of the velar flange has been observed, and the point where the flange changes into a ridge lies more dorsally.

To judge from the figure published by KRAUSE (1889, Pl. II, Fig. 5) the lectotype of *S. linnarssoni* is beyond doubt conspecific with the specimens from the *Schroeteri* and *Crassicauda* limestones of Sweden. It is, however, difficult without an examination of the original specimen to decide if the specimen figured by him on Pl. II, Fig. 4 belongs to this species. The arrangement of the crests of this specimen rather suggests *S. multimarginata*. It is very difficult to decide if other only reported occurrences of *S. linnarssoni* belong to it. KUMMEROW (1939) certainly has referred to *S. linnarssoni* a mixture of different species, including *S. costata*.

OCCURRENCE.—*Steusloffia linnarssoni* has been found in the *Schroeteri* and the *Crassicauda* beds. In some districts it is a fairly common species.

Öland.—Böda Hamn bore (3 specim.); Gammalsby bore (20 specim.). *South Bothnian area.*—Erken, boulder no. 10. *Siljan district.*—Furudal, quarry at the rivulet Kalkbergsbäcken (3 specim.); Kårgärde (6 specim.); Vikarbyn (2 specim.); Fjäcka (4 specim.). *Östergötland.*—Motala bore (44 specim.); Smedsby Gård bore (23 specim.). *Västergötland.*—Norra Skagen bore (14 specim.); Stora Åsbotorp bore (3 specim.).

Steusloffia multimarginata ÖPIK, 1937

Pl. X, Figs. 11–14; Text-figs. 39, 40C.

? 1889 *Strepula linnarssoni* n.sp.—KRAUSE, p. 16, Pl. II, Fig. 4 (non Pl. II, Fig. 5 = lectotype of *S. linnarssoni* KRAUSE, 1889).

? 1908 *Beyrichia* (*Steusloffia*) *linnarssoni* KRAUSE—ULRICH & BASSLER, p. 282, Text-fig. 8 (copied from KRAUSE, 1889, Pl. II, Fig. 4).

? 1937 *Steusloffia linnarssoni* (KRAUSE)—ÖPIK, p. 50, Text-fig. 7 (diagram after KRAUSE, 1889, Pl. II, Fig. 4), p. 51.

1937 *Steusloffia multimarginata* n.sp.—ÖPIK, p. 52, Pl. IV, Fig. 4, Pl. XIV, Fig. 1.

? 1939 *Steusloffia linnarssoni* (KRAUSE)—KUMMEROW, p. 92, Fig. 14 (copied after ÖPIK 1937, Text-fig. 7).

1939 *Steusloffia linnarssoni* (KRAUSE)—KUMMEROW, p. 95, Fig. 20 (diagram after ÖPIK 1937, Pl. IV, Fig. 4).

1940 *Steusloffia costata* (LINNARSSON)—THORSLUND, pp. 176–178, Text-fig. 58, Pl. 2, Fig. 10, Pl. 3, Figs. 1–7 [non Pl. 2, Fig. 12 = *S. costata* (LINNARSSON) and Pl. 2, Fig. 11 = *S.* cf. *costata* (LINNARSSON)].

1948 *Steusloffia* aff. *costata* (LINRS.)—THORSLUND, pp. 344, 360, 369 (partim).

1953a *Steusloffia costata* (LINNARSSON)—HENNINGSMOEN, p. 45 (partim), ? Pl. 1, Fig. 8.

1955 *Steusloffia multimarginata* ÖPIK—SARV, p. 16.

1956a *Steusloffia multimarginata* ÖPIK—SARV, p. 52.

Holotype.—Right valve, TM no. Os-2243, figured by Öpik 1937, Pl. IV, Fig. 4.

Type Locality.—Estonia, Kohtla-Järve.

Type Stratum.—Kohtla zone of the Kukruse Stage ($C_{II}\alpha$).

Diagnosis.—The branching point lies at about the transversal line through the middle of the presulcal knob. C3v is more or less posteriorly or slightly posterodorsally directed, its anterior part almost parallel to C4. C3 divided into a dorsal and a ventral branch. The velar flange ends posteriorly rather abruptly at about the longitudinal line through the top of the posteroventral lobe.

Description.—The branching point of the crests lies at about the transversal line throught the middle of the presulcal knob or very slightly in front of it. C3v runs in more or less longitudinal direction, its posterior part curving slightly posterodorsally and terminating in a little node on the top of the posteroventral lobe. C4 behind the branching point almost parallel to C3v, more or less longitudinally directed. Posteriorly C4 turns around the ventral lobe and runs up to the dorsal plica in almost transversal direction. C3d always developed, dorsally coalescent with the dorsal plica, ventrally as a rule reaching the dorsal end of the posteroventral lobe. C2 confined to the presulcal knob.

Dorsal plica, if well preserved, only a little higher than the crests, projecting slightly beyond the hinge-line. Close to the anterior cardinal corner field a small, smooth node present in most, but apparently not in all specimens.

The velar flange ends posteriorly rather abruptly at about the longitudinal line through the top of the posteroventral lobe, and continues dorsally from that point as a velar ridge. This becomes rather weak and bend-like near the cardinal corner and continues, without any apparent interruption, into the dorsal plica.

In well preserved specimens the whole external surface of the valve is very minutely granulate. Between these granules rather large tubercles are scattered except in the sulcus, and between the sulcus and the dorsal margin. Velar flange with a fine radial striation in the best preserved specimens, and faintly undulate in some valves.

Larval instars with only a partial development of the crests were described by Thorslund (1940, p. 177, Fig. 58, Pl. 3, Figs. 2, 3, 4). In specimens with a length (excl. velum) of 1.63–1.68 mm C4 is not developed. In a specimen with a length of 1.99 mm C4 is already present. No distinct correspondence could be observed by the present writer in the arrangement of the tubercles and the course of C4 in specimens, where the latter is not developed.

Dimensions.—See Table 28.

Discussion.—The holotype of *S. multimarginata* is similar in all important respects to the Swedish specimens described. The arrangement of the tubercles in a row ventral of C4, which by Öpik (1937, p. 52) was regarded to be a specific character, occurs also in some specimens from Tvären (Pl. X, Fig. 12; Thorslund 1940, Pl. 2, Fig. 10). On the whole, the details of the arrangement of the tubercles seem to vary rather considerably among the specimens studied.

Table 28.

No.	Mus. cat. no.	L. valve	H. valve	L. domic.	H. domic.	Valve	Locality	Remarks
1	SGU	2.61	1.57	2.27	1.27	l	1.2 km W of Tandsbyn station	Thorslund 1940, Pl. 3, Fig. 6.
2	UM D423	—	—	2.43	1.51	r	Fjäcka, loc. 6	
3	UM D424	—	~1.40	2.03	1.18	r	Fjäcka, loc. 7	Figured on Pl. X, Fig. 11.
4	UM T 19	—	1.49	2.21	1.28	l	Tvären, Ringsö	Thorslund 1940, Pl. 2, Fig. 10.
5	UM T 24	~2.05	1.33	1.99	1.15	l	„ „	Thorslund 1940, Pl. 3, Fig. 4.
6	UM T 22	—	—	1.68	0.94	r	„ „	Thorslund 1940, Pl. 3, Fig. 2.
7	UM T 76	1.77	1.08	1.67	0.95	r	„ „	Figured on Pl. X, Fig. 14.
8	UM T 23	~1.76	1.09	1.63	0.92	r	„ „	Pl. X, Fig. 13. Thorslund 1940, Pl. 3, Fig. 3.
9	UM T 175	1.44	—	1.38	0.74	r	„ „	

The species described differs from *S. rigida* Öpik by the more posterior position of the branching point of the crests, the direction of the anterior part of C3v, by C2 being confined to the presulcal knob, and by a more dorsal position of the posterior end of the velar flange.

Occurrence.—*Steusloffia multimarginata* seems to have a rather restricted vertical distribution, all finds made so far coming from the lowermost part of the *Ludibundus* beds or contemporaneous strata. In Estonia it occurs in the Kohtla zone of the Kukruse Stage ($C_{II}\alpha$, cf. Sarv 1956a) and in the Oslo region in the *Ampyx* beds ($4a\beta$).

Estonia (cf. Öpik 1937; Sarv 1956a). *Södermanland*, Tvären area.—Erratic boulders (12 specim.). *Jämtland*, Lockne area.—Exposure 1.2 km W of the Tandsbyn railway station (cf. Thorslund 1940, Pl. 3, Fig. 6). *Siljan district*.—Fjäcka, locality no. 7 (5 specim.); Kårgärde (1 specim.). *Öland*.—Böda Hamn bore (1 specim.). *Östergötland*.—Smedsby Gård bore (6 specim.). *Västergötland*.—Kullatorp bore (1 specim.); Norra Skagen bore (2 specim.); Stora Åsbotorp bore (4 specim.). *Oslo region*.—Skogsfaret, Ullernåsen (OM no. 66754).

Steusloffia costata (Linnarsson, 1869)

Pl. X, Figs. 15–18, Pl. XI, Fig. 1; Text-fig. 40A.

1869a *Beyrichia costata* n.—Linnarsson, p. 196.
1869b *Beyrichia costata* n.sp.—Linnarsson, p. 85, Pl. II, Figs. 67–68.
1869 *Beyrichia bilobata* n.sp.—Kolmodin, p. 20, Fig. 13.

1901 *Beyrichia costata* LINNARSSON—HOLM, p. 56, Figs. 50a, b (copied from LINNARSSON 1869b, Pl. II, Figs. 67–68).
1934 *Strepula ? costata* (LINNARSSON)—BASSLER & KELLETT, p. 477.
1939 *Steusloffia linnarssoni* (KRAUSE)—KUMMEROW, p. 93, Fig. 17.
1940 *Steusloffia costata* (LINNARSSON)—THORSLUND, Pl. 2, Fig. 12 [non Pl. 2, Fig. 10, Pl. 3, Figs. 1–7 = *Steusloffia multimarginata* ÖPIK, 1937; Pl. 2, Fig. 11 = *S.* cf. *costata* (LINNARSSON)].
1943 *Steusloffia costata* (LINRS.)—WESTERGÅRD, p. 76, Figs. 59a, b (copied from LINNARSSON 1869b, Pl. II, Figs. 67–68), p. 78.
1948 *Steusloffia costata* (LINNARSSON)—THORSLUND, p. 268, Pl. XX, Fig. 10.
1948 *Steusloffia* aff. *costata* (LINRS.)—THORSLUND, pp. 350, 359, 360 (partim).

TYPE.—The original specimens of LINNARSSON could not be found in the Museum of SGU, and a neotype must apparently be chosen. No suitable material from the localities mentioned by LINNARSSON (1869b, p. 85) has, however, been at the present writer's disposal, and the designation of a neotype must, therefore, be postponed. There is, however, no question about the identity of the species described by LINNARSSON (1869a, 1869b) as he gives a rather detailed account of the arrangement of the crests.

TYPE REGION.—Västergötland.

TYPE STRATUM.—Middle or upper part of the *Ludibundus* beds.

DIAGNOSIS.—The branching point of the crests lies at about the longitudinal line through the ventral end of the presulcal knob or slightly more ventrally. C3v and C4 more or less parallel to each other ventrally. C3 divided into a dorsal and a ventral branch. The dorsal ends of C3d and C4 united with each other and not reaching the dorsal plica. Dorsal plica projecting strongly beyond the hinge-line. Posteriorly the velar flange ends abruptly somewhat ventrally of the longitudinal line through the top of the posteroventral lobe.

DESCRIPTION.—Posteroventral lobe relatively narrow, dorsal end of it reaching to about the longitudinal line through the middle of the presulcal knob. The top of the lobe is only slightly higher than that of the presulcal knob.

The branching point of the crests lies in front of the presulcal knob, usually at about the longitudinal line through the ventral end of the knob or slightly more ventrally. C1 and C3v form a continuous curve which surrounds the presulcal knob and the ventral end of the sulcus, ending in a small node on the top of the posteroventral lobe. At the branching point C4 turns in anterior direction almost perpendicularly to the other crests, then curves backwards more or less parallel to C3v, rounds the posteroventral lobe, and continues dorsally in more or less transversal direction. C4 and C3d are united at their dorsal ends, neither of them reaching the dorsal plica. The distance between the united dorsal ends of C4 and C3d and the dorsal plica is, however, rather small. C3d is as a rule rather short, not quite reaching the dorsal end of the posteroventral lobe. C2 confined to the presulcal knob.

Table 29.

No.	UM Mus. cat. no.	L. valve	H. valve	L. domic.	H. domic.	Valve	Locality	Remarks
1	D 422	2.41	1.61	2.26	1.36	r	Fjäcka, loc. 7	Figured on Pl. X, Fig. 15.
2	Vg. 83	3.24	2.08	~2.92	~1.75	r	Kullatorp 66.03 m	
3	Vg. 81	3.13	1.99	~2.80	~1.75	l	Kullatorp 70.52 m	
4	Vg. 22	~2.95	~1.85	~2.81	1.72	r	Kullatorp 71.03 m	Thorslund 1948, Pl. XX, Fig. 10.
5	Vg. 78	2.73	1.73	—	1.49	l	Kullatorp 71.03 m	Figured on Pl. X, Fig. 18; Pl. XI, Fig. 1; Text-Fig. 41.
6	Vg. 82	2.63	1.68	2.37	1.41	r	Kullatorp 66.03 m	
7	Vg. 80	2.26	1.56	2.09	~1.31	r	Kullatorp 65.81 m	
8	Vg. 79	1.95	1.31	—	—	r	Kullatorp 71.03 m	Figured on Pl. X, Figs. 16–17.

The dorsal plica is flattened posteriorly and anteriorly, and protrudes beyond the hinge-line as a pair of thin, blade-like extensions which are rather easily fractured. In the middle the dorsal plica runs, as usual in *Steusloffia*, in a ventrally directed curve, and is there of about the same shape as the crests. Most specimens examined have a node on the posterior cardinal corner field.

Velar flange anteriorly much as in the other two species described, confluent with the dorsal plica. Its posterior end is truncated and situated somewhat ventrally of the longitudinal line through the top of the posteroventral lobe. Dorsal to this point the velar structure continues as a velar ridge becoming weaker dorsally and being formed like a bend before its confluence with the dorsal plica. For the ventral margin of the velar flange, cf. p. 363.

Ornamentation on the whole as in *S. multimarginata*, but the tubercles generally slightly smaller, and the minute granules between them coarser.

On the small specimen figured on Pl. X, Figs. 16–17 (length of the valve 1.95 mm) C3d and the posterior part of C4 are not developed, otherwise, excepting the simple ventral margin of the velum, it is similar to the large specimens.

Dimensions.—See Table 29.

Discussion.—The discovery of the type specimens of *Beyrichia bilobata* Kolmodin, 1869, by Dr. A. Martinsson in UM has shown this species to be conspecific with *S. costata*. Kolmodin figured and described only internal moulds of his species, and if only these were known *B. bilobata* would have been quite indeterminable. The slab of rock with the internal moulds described by him contains, however, also several external imprints of valves showing clearly the arrangement of the crests of *S. costata*. Linnarsson's (1869a) and Kolmodin's (1869) papers were issued in the same year. For Linnarsson's

paper no more precise date of publication than the first half of 1869 could be obtained. KOLMODIN's paper was printed some weeks before May 24th, 1869, at which date his disputation for the degree of Doctor of Philosophy took place. On account of the impossibility of establishing a more exact date of publication of LINNARSSON's paper the specific name *bilobata* KOLMODIN thus seems to have priority over *costata* LINNARSSON. As, however, the latter name is well-known and has been widely used in literature, and as the description by LINNARSSON (1869b) is quite sufficient for the determination of the species, which cannot be said of that by KOLMODIN, it seems advisable to preserve the specific name *costata* for this species. In order to do this an application for suppression of the specific name *bilobata* KOLMODIN, 1869, as published in the combination of *Beyrichia bilobata*, must be submitted to the International Commission on Zoological Nomenclature.

Steusloffia costata differs rather clearly from the other species of *Steusloffia* described here, especially by the anterior position of the branching point of the crests, the broad (tr.), blade-like dorsal plica, and by the ventral position of the truncated posterior termination of the velar flange. Futhermore, the dorsal ends of C4 and C3d are confluent, and do not reach the dorsal plica. *S. rigida* ÖPIK seems to be the most closely similar species. It differs by the more ventrally placed branching point, by independent coalescence of C4 and C3d with the dorsal plica, and by C2 being developed also dorsally of the presulcal knob. The posterior end of the velar flange seems, however, to have a similar position as in *S. costata* to judge from the specimen on Pl. VI, Fig. 2, in ÖPIK (1937).

The specimen from the Upper *Chasmops* (= *Macrourus*) beds figured by THORSLUND (1940, Pl. 2, Fig. 11) differs in certain details from the specimens from the *Ludibundus* limestone, particularly by the more anterior position of the branching point in the crests. Until more material from the *Macrourus* formation has been studied it would be better to regard this specimen as *S.* cf. *costata*.

OCCURRENCE.—*Steusloffia costata* occurs through the whole extension of the *Ludibundus* beds, except, perhaps, in their lowermost layers. A very similar or possibly identical species has been found in the *Macrourus* beds (cf. above).

Västergötland.—Kullatorp bore (36 specim.); Norra Skagen bore (2 specim.); Mossen, Kinnekulle (numerous specim.); Ållebergsände (numerous specim.). *Siljan district*.—Fjäcka, localities 7–8 (7 specim.); Amtjärn (2 specim.). *Jämtland*, Lockne area.—Exposure 1.2 km W of Tandsbyn railway station. *Skåne*, Fågelsång district.—Erratic boulders NNO of Sularp Gård, locality no. E 56 (1 specim.).

Superfam. HOLLINACEA Swartz, 1936

[*Nom. transl.* Jaanusson, herein (*ex Hollinidae* Swartz, 1936)]

Diagnosis.—Histial structure present at least in heteromorphs. Early genera with histial as well as velar structures. Most genera exhibit a well defined histial dimorphism.

Families.—*Hollinidae* Swartz, 1936
Tetradellidae Swartz, 1936
Sigmoopsidae Henningsmoen, 1953
Oepikiumidae nov.
? *Acronotellidae* Swartz, 1936.

Discussion.—The reasons for including these families in a separate superfamily are discussed on pp. 217–218.

In an attempt to visualize the possible ancestors of the hollinaceans the following four cases seem to deserve attention: (1) Eurychilinacean-like velate, non-dimorphic forms from which the hollinaceans may have been derived by the development of a new, dimorphic adventral structure. (2) Eurychilinacean-like forms as those in (1), but with a velar dimorphism; the development towards the hollinaceans implied formation of a new, dimorphic adventral structure and simultaneous loss of the ability to produce a velar dimorphism. (3) Non-dimorphic forms with both a velar and a histial structure from which the hollinaceans and the eurychilinaceans may have been derived, by acquisition of the ability of producing a histial, and a velar dimorphism, respectively; this involves secondary reduction of the histial structure in the eurychilinaceans. (4) Non-dimorphic, non-velate, and non-histiate forms like early leperditellaceans from which the hollinaceans may have been developed independently of the eurychilinaceans by the formation of a dimorphic histial structure and also of a further adventral structure between the histial structure and the free edge; in this case the sigmoopsid and tetradellid velar structure would not be strictly homologous with that of the eurychilinaceans.

At our present state of knowledge the first of these possibilities seems to be the most probable. The velar structure, especially in tecnomorphs of certain sigmoopsids and tetradellids, is in all respects so similar to that of the eurychilinaceans that its velar origin does not seem subject to any doubt. No eurychilinacean with a real histial structure is known so far, and there is thus no evidence that this structure has once existed, but has undergone complete reduction. Also the second possibility must, however, be taken into serious account, since several sigmoopsids are known (e.g. *Carinobolbina*) in which the tecnomorphs possess no adventral or only a histial structure, whereas the heteromorphs have both velar and histial flanges; whether this implies di-

morphism of both these structures cannot, however, be ascertained at present (cf. p. 396).

The interrelation of the hollinacean families is still not quite clear. *Sigmoopsidae* appear in several respects to be the most primitive group, and may have given rise to the other families. The main difference between the *Tetradellidae* and the *Sigmoopsidae* lies in the presence of the heteromorphic loculi in the former family, and thus is on the whole identical with that between *Ctenoloculininae* (cf. JAANUSSON & MARTINSSON 1956) and *Hollininae* of the family *Hollinidae*. It is therefore possible that sigmoopsids ought to be regarded merely as a subfamily of *Tetradellidae*. The close relation of tetradellids and sigmoopsids becomes especially conspicuous on comparison of simple, unisulcate members of these groups, as for instance *Dilobella* and *Sigmobolbina*, which differ from each other mainly by the presence or absence of the loculi in the heteromorphs. Nevertheless, until the phylogenetic relations between tetradellids and sigmoopsids are better understood, the present writer, following HENNINGSMOEN (1953a), regards these groups as separate families.

The Upper Ordovician genus *Foramenella* STUMBUR, 1956, is probably a specialized off-shoot of the tetradellids. This unisulcate genus has neither a velar nor a histial structure in either dimorph, and the dimorphism is manifested only by the development of five distinct loculi in heteromorphs (STUMBUR 1956, Pl. I, Figs. 4, 6, 7). The sulcus is long and sigmoidal as in *Dilobella* and in the unisulcate sigmoopsids, and the general appearance of the carapace is decidedly of sigmoopsid type. By its distinct loculi in the heteromorphs *Foramenella* reminds of the unisulcate ctenoloculine genera *Bisacculus* and *Tetrasacculus* which have poorly developed histial structure, and thereby differ from the other hollinids. It does not seem excluded that *Foramenella* may be related to these Devonian genera which by later studies may be proved to belong to a separate branch of the hollinaceans derived from the tetradellids by reduction of the adventral structures. The loculi in *Foramenella* are, on the other hand, considerably smaller than those of *Bisacculus* and *Tetrasacculus* and are situated at the same level as the loculi of the tetradellids, i.e. laterally of the level of the velar structure. This condition suggests that the reduction of the adventral structures in *Foramenella* may have taken place independently from the Devonian genera mentioned above, the similarities between them being due to a homoeomorphic development. In the present paper *Foramenella* is provisionally included in *Tetradellidae*.

The hollinids very likely developed from sigmoopsids or sigmoopsid-like ancestors by the acquisition of certain special hollinid characters such as the abrupt posterior end of the histial dolon, the common presence of spurs, and the bulbous dorsal part of L3. The velar structure is always lacking, and the subhistial field is somewhat lower (tr.) than in most sigmoopsids. Certain simple hollinids resemble unisulcate sigmoopsids or tetradellids to such an extent that it is difficult to draw a sharp limit. In the present paper the abrupt

posterior ending of the histial dolon and/or the presence of one or two pairs of histial spurs in tecnomorphs have been regarded as diagnostic for the family *Hollinidae*. For this reason the Ordovician and Silurian genus *Grammolomatella* is included here in the hollinids. Also these characters are, however, not restricted to *Hollinidae*. An abrupt posterior margin of the histial dolon occurs also in *Sigmobolbina monoceratina* n.nom. and in *Oepikium*. The ctenoloculine genera *Bisacculus* and *Tetrasacculus*, on the other hand, lack an abrupt posterior margin of the dolonal flange. As long as the Upper Ordovician and Silurian hollinaceans are poorly known the delimination of the hollinacean families remains somewhat uncertain.

The genus *Oepikium* agrees with *Hollinidae* in the extension of the frill. Differences from all other hollinaceans are, however, found in the construction of the frill, its width in tecnomorphs, and in the wide, strongly convex dolon. The dimorphism of this genus reminds more of that of certain eurychilinids, as *Cystomatochilina*, than of any other hollinacean. In view of these differences *Oepikium* is placed here into a separate hollinacean family. It probably represents an early, specialized off-shoot from the sigmoopsids, close to the point of divergence between sigmoopsids and hollinids.

Apart from the families included above in *Hollinacea* there exist also certain other groups of palaeocope ostracodes which are at present incompletely known and therefore difficult to classify, but which may belong to *Hollinacea*. The subfamily *Graviinae* Polenova, 1952 (originally referred to *Acronotellidae*), may represent simple hollinids, but as long as the presence and type of its probable dimorphism has not been established the taxonomic position of this subfamily remains uncertain. The various Upper Devonian genera included by Zaspelova (1952) in *Drepanellidae* form a puzzling assemblage of different, in part probably unrelated forms none of which appears to be a real drepanellid. Certain characters of *Neodrepanella* and allied genera (subfam. *Neodrepanellinae* Zaspelova, 1952), particularly the shape and position of the spurs, and the development of the dorsal part of L3, are so similar to those of hollinines that the presence in these genera of a hollinid type of dimorphism is strongly suspected. These species require a further study before they can be properly classified.

Occurrence.—The earliest known member of *Hollinacea* is a new species of *Glossomorphites* from the lower Arenigian of Sweden (cf. Tjernvik 1956, p. 163). The latest hollinids are recorded from Permian strata.

Fam. SIGMOOPSIDAE Henningsmoen, 1953

Diagnosis.—Nonsulcate to quadrilobate, mostly with pronounced preplete outline and very low to non-existent dorsum. Early genera with velar and histial structure in both dimorphs, or with only velar structure in tecnomorphs, later genera without velar structure. Histial dimorphism of the non-locular

type. The lateral surface and the posterior end of the histial dolon tend to merge smoothly into the lateral surface of the domicilium. Dorsal part of L3, if developed, not broadly bulbous, ventral part of S3 usually more persistent than the dorsal part.

GENERA.—*Polyceratella* ÖPIK, 1937
Winchellatia KAY, 1940
Aulacopsis HESSLAND, 1949
Sigmoopsis HENNINGSMOEN, 1953
Sigmobolbina HENNINGSMOEN, 1953
Carinobolbina HENNINGSMOEN, 1953
Glossomorphites HESSLAND, 1953
Lomatobolbina n. gen.
Oecematobolbina n. gen.

HENNINGSMOEN (1953a) tentatively included also *Ctenobolbina* ULRICH, 1890, in *Sigmoopsidae*. As long as the dimorphism of the type species of this genus has not been described the taxonomic position of *Ctenobolbina* remains uncertain. Also *Ogmoopsis* HESSLAND, 1949, may belong to this family, as suggested by HENNINGSMOEN (1953a), but its dimorphism, if present, is hitherto unknown. Two further genera, *Bolbina* and *Kiesowia*, included by HENNINGSMOEN (1953a) in *Sigmoopsidae*, belong in the light of the material studied to *Piretellidae* and *Quadrijugatorinae*, respectively. Certain characters of *Ullerella* HENNINGSMOEN, 1950, as for instance the high subhistial (?) field, the outline of the valve, and the very low dorsum, suggest sigmoopsid affinities. This genus is incompletely known at present (only internal moulds and external impressions have been found), and more material should be studied in order to ascertain its taxonomic position.

DISCUSSION.—HENNINGSMOEN (1953a) subdivided *Sigmoopsidae* into two subfamilies: *Sigmoopsinae* and *Glossopsinae* (= *Glossomorphitinae* HESSLAND, 1953). The characters used by him in distinguishing between them were the shape of S2 and L3, and the presence or absence of a prominent velar structure. There is no doubt that *Glossomorphites* and *Aulacopsis* are more closely related to each other than to the other sigmoopsid genera, but in the light of the new material the differences between *Glossomorphitinae* and the genera included by HENNINGSMOEN in *Sigmoopsinae* do not appear distinct enough to justify a subdivision into separate subfamilies. The small differences in the shape of S2 and L3 do not seem to be of quite as great importance as thought by him, and the new genera described in the present paper seem in some respects to take an intermediate position between these subfamilies. Until more material has been described of this rather homogeneous family it seems more appropriate to regard the latter as comprising a single subfamily.

As pointed out on p. 218 the ventral view of the type species of *Acronotella* exhibits a considerable similarity to that of certain sigmoopsids, and the

possibility should be taken into account that *Sigmoopsidae* may represent a junior synonym to *Acronotellidae* SWARTZ, 1936.

OCCURRENCE.—The earliest known sigmoopsid occurs in the lower Arenigian of Sweden (*Glossomorphites* n.sp., cf. TJERNVIK 1956, p. 163). From post-Ordovician strata no species referable with certainty to this family is known at present.

Gen. *Sigmoopsis* HENNINGSMOEN, 1953

TYPE SPECIES.—*Ceratopsis platyceras* ÖPIK, 1937.

DIAGNOSIS.—Quadrilobate; ventral part of L1, when developed, as a rule narrow, dorsal part bulbous or produced into a speral spine. Dorsal part of S1, when developed, narrow, constricted between the bulbous dorsal part of L1 and the ventral end of L2. S2 long, extending ventrally to the histium. S3 of varying width, occasionally obsolete dorsally. A distinct velar ridge always present. Tecnomorphs with a histial ridge, heteromorphs with a flange-like histial dolon.

SPECIES.—*Beyrichia obliquejugata* FR. SCHMIDT, 1858
Beyrichia (*Ctenobolbina*) *rostrata* KRAUSE, 1892
Ctenobolbina rostrata var. *cornuta* KRAUSE, 1896
Ceratopsis perpunctata ÖPIK, 1937
Ceratopsis perpunctata prominens ÖPIK, 1937
Ceratopsis platyceras ÖPIK, 1937
Ceratopsis granulata SARV, 1956
Sigmoopsis bergsbrunnae n.sp.

ÖPIK (1937, p. 25) pointed out that *Ceratopsis schmidti* BONNEMA, 1909, is a junior synonym of *Beyrichia obliquejugata* FR. SCHMIDT, 1858. The present writer has examined a number of well-preserved specimens of this species from the Kukruse Stage of Estonia, and he entirely agrees with ÖPIK that the characters stated by ÖPIK as common to SCHMIDT's type specimen and the specimens figured by BONNEMA are so characteristic for the species in question as to leave practically no doubt as to the identity of *S. schmidti* and *S. obliquejugata*.

As pointed out by J. G. ANDERSSON (1893, p. 127) and confirmed by an examination of his material by the present writer *Beyrichia carinata* KRAUSE, 1892, is conspecific with *Beyrichia rostrata* KRAUSE, 1892. The former species is erected on tecnomorphs, and the latter on heteromorphs of the same species.

The present writer fails to understand the statement by HENNINGSMOEN (1953a, p. 205) to the effect that also *S. platyceras* may be a synonym of *S. obliquejugata* provided the latter species is identical with *S. schmidti*. The examination of a number of well-preserved specimens of *S. platyceras* has shown that it is a well-defined species and clearly different from *S. obliquejugata*.

GENERIC CHARACTERS.—In *Sigmoopsis* the details of the sulcation and lobation exhibit on the whole a more constant development than in *Glossomorphites*.

The dorsal end of S1 is usually constricted between the speral process and the dorsal part of L2. The ventral part of S1 is as a rule expanded except for *S. platyceras* in which it is obsolete (cf. Öpik 1937, Pl. II, Figs. 6, 7). S2 has an almost uniform shape in all species, being long (tr.), somewhat sigmoidal, and of almost equal width along its whole extension or slightly tapering ventrally. S3 may have a width equal to that of S2 or be narrower and shallower than S2, as in *S. platyceras* and *S.* sp. B. The ventral part of L1 is usually expanded forming a speral process, produced into a spine in some species. The shape and convexity of the speral process appear to be constant within a species, and supply some of the best specific characters. Ventral part of L1 as a rule narrow, usually ridge-like, ventrally continuous with the histial ridge. The ridge of the ventral part of L1 may continue along the margin of the lateral surface of the speral process, and within a species the degree of its dorsal extension seems to be fairly constant. L2 is as a rule broad ventrally and narrow dorsally, becoming obsolete at about the longitudinal mid-line of the speral process or slightly ventrally of this point. L3 usually well defined and of almost uniform width along its whole extension. L4 as a rule flattened, expanding in posterodorsal direction. On the whole the shape of sulci and lobes is constant within a species, and supply good specific characters.

A ridge-like, prominent velar structure is invariably present. In both dimorphs the histial structure has a development very similar to that of *Glossomorphites*. The dorsal boundary of the histial ridge in tecnomorphs is, however, usually better defined than that of the latter genus, especially the boundary between the histial structure and L3 which is often formed by a furrow. In *Glossomorphites* the histial structure is on the whole slightly thicker and more solid than that of *Sigmoopsis*.

Discussion.—The general shape of the lobes of *Sigmoopsis* resembles that of *Glossomorphites*. The former genus differs by the following main characters: (1) L2 is always considerably shorter than the other lobes; (2) the dorsal part of L1 is usually expanded and the ventral part narrow; (3) the dorsal part of S1, if developed, is considerably constricted between the dorsal parts of L1 and L2; (4) a prominent velar structure is invariably present.

Occurrence.—The earliest known species of *Sigmoopsis* appear in the Middle Ordovician Uhaku (C_1c) Stage (Upper Llandeilian) of Estonia and in the contemporaneous *Crassicauda* limestone of Sweden. The latest species occurs in the Upper Ordovician Rakvere Stage (E) of Estonia (*S. granulatum*). Outside of Baltoscandia the genus is unknown so far.

Sigmoopsis platyceras (Öpik, 1937)

Pl. XI, Figs. 7–8; Text-fig. 5A.

1937 *Ceratopsis platyceras* n.sp.—Öpik, p. 26, Pl. II, Figs. 6–7, Pl. X, Figs. 12–14, Pl. XIV, Fig. 5.

1951c *Ceratopsis platyceras* Öpik—Kesling, Pl. VI, Figs. 2–3 (after Öpik 1937).

1953a *Sigmoopsis platyceras* (Öpik)—Henningsmoen, pp. 204–205, Fig. 5 (from Kesling 1951 c).
1955 *Ceratopsis platyceras* Öpik—Sarv, p. 15.
1956 a *Ceratopsis platyceras* Öpik—Sarv, p. 47.

Holotype.—Right heteromorphic valve (TM), figured by Öpik 1937, Pl. II, Fig. 6.

Type Locality.—Estonia, Kohtla-Järve.

Type Stratum.—Kukruse Stage, probably its lower zone ($C_{II}\alpha$).

Diagnosis.—Length of the heteromorphs 1.6–1.7 mm. Speral process flattened, highest at its posterior end, merging in anterior and ventral direction imperceptibly into the surface of the valve. L3 broad, moderately convex, of almost uniform width. S3 narrow, fairly shallow. L4 flattened, almost obsolete. Lobes smooth, without any distinct ornamentation.

Discussion.—This species has previously not been recorded from Sweden. The tecnomorphs figured are the only Swedish specimens known. *Sigmoopsis platyceras* has been well illustrated by Öpik (1937), and the Swedish material does not contribute to the knowledge of its characters.

Occurrence.—According to Sarv (1956a) *S. platyceras* occurs in Estonia in the lower part of the Uhaku Stage ($C_I c\alpha$) and in the Kukruse Stage (C_{II}). Its occurrence in $C_I c$ needs, however, further confirmation. The Swedish specimens have been found in the middle part of the *Ludibundus* limestone.

Estonia (cf. Sarv 1956a). *Sweden*, Siljan district, Fjäcka, locality no. 8.

Sigmoopsis bergsbrunnae n. sp.

Pl. XI, Figs. 2–6; Text-fig. 41.

1948 *Ceratopsis* aff. *perpunctata prominens* Öpik—Thorslund, p. 360.

Holotype.—Right heteromorphic valve, UM no. B 282, figured on Pl. XI, Fig. 5.

Type Region.—South Bothnian area. The holotype was found in the erratic boulder Bergsbrunna no. 1.

Type Stratum.—Uppermost *Crassicauda* limestone.

Derivation of the Name.—After Bergsbrunna, the locality in Uppland where the type boulder was found.

Diagnosis.—Length of the heteromorphs 1.02–1.18 mm. Speral process knob-like, oblong, highest dorsally, its dorsal margin slightly convex, not protruding beyond the dorsal margin of the valve, its lateral side more or less flattened and sloping in ventromedian direction. The top of the speral process forms the highest point of the valve. S3 about as broad as S2. Lobes ornamented with rather coarse pits.

Description.—Dorsal part of L1 expanded into a knob-like speral process, ventral part narrow, ridge-like, continuing in a ridge along the anterior margin

of the lateral surface of the speral knob. The knob is slightly oblong in antero-ventral direction, its dorsal end reaching in most specimens the dorsal margin of the valve, but never protruding beyond it. Dorsal side of the knob convex, steeply sloping; lateral side flattened, gently sloping in ventromedian direction. The top of the speral knob forms the highest point of the valve. Ventral part of L2 expanded, dorsal part narrow, curved, its dorsal end extending roughly up to the longitudinal line through the middle of the speral knob or slightly more dorsally. L2 on the whole comparatively flat, its summit much lower than that of L3. L3 relatively narrow, slightly constricted close to its ventral part and the dorsal end somewhat expanded; highest convexity slightly ventral of the middle of the lobe. L4 ventrally about as broad as the broadest part of L3, expanding in posterodorsal direction, rather high ventrally, flattened dorsally. The highest point of L4 is situated at about the posterior end of the histial ridge, being only slightly lower than that of L3. S1 narrow and rather shallow. S2 and S3 of about equal width, depth, and length (tr.), the ventral ends of both sulci reaching the histium.

Tecnomorphs with a narrow histial ridge which is continuous anteriorly with the dorsal part of L1, and becomes obsolete posteriorly at about the mid-height of the valve or slightly dorsally of it. Heteromorphs with a moderately broad, thick, flange-like histial dolon strongly protruding ventrally. Both dimorphs with a distinct velar ridge extending anteriorly almost up to the anterior cardinal corner and posteriorly to about the posterior end of the histial structure.

Lateral surface of the lobes covered with rather coarse pits.

Dimensions.—See Table 30.

Table 30.

No.	UM Mus. cat. no.	L. valve	H. valve	H-L	Valve	Locality	Remarks
1	B 298	—	0.71	—	h—l	Erken no. 10	
2	B 297	1.13	0.68	0.97	h—l	,, ,, ,,	Figured on Pl. XI, Fig. 3.
3	B 282	1.03	0.65	—	h—r	Bergsbrunna no. 1	Holotype. Pl. XI, Fig. 5.
4	B 281	1.03	0.63	—	h—r	,, ,, ,,	Figured on Pl. XI, Fig. 4.
5	B 284	~1.07	0.61	—	t—l	,, ,, ,,	
6	B 283	1.06	0.58	—	t—r	,, ,, ,,	Figured on Pl. XI, Fig. 2.

Discussion.—At first sight *S. bergsbrunnae* n. sp. appears to be almost identical with *S. perpunctata* (Öpik). A closer comparison reveals, however, distinct and constant differences between these species. The main differences lie in the much higher speral knob and in the absence of distinct smooth borders around the lobes in *S. bergsbrunnae*.

Occurrence.—*Sigmoopsis bergsbrunnae* n. sp. has been found only in the *Crassicauda* limestone.

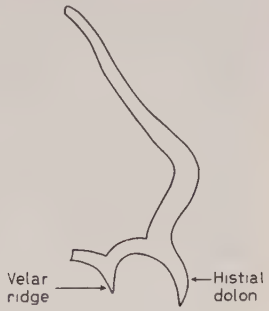


Fig. 41. *Sigmoopsis bergsbrunnae* n. sp. Diagrammatic drawing of a transversal section of a heteromorph. After a thin section. × 50.

South Bothnian area.—Erratic boulders Bergsbrunna no. 1 (6 heterom., 5 tecnom.) and Erken no. 10 (2 heterom.). *Västergötland*, Kinnekulle.—Norra Skagen bore (1 heterom.). *Siljan district.*—Furudal, quarry at the rivulet Kalkbergsbäcken (1 heterom.).

Sigmoopsis sp. A

Pl. XI, Fig. 9.

1940 *Ceratopsis obliquejugata* (Fr. Schmidt)—Thorslund, pp. 170–171, Pl. 3, Fig. 13.

Description.—Only one tecnomorphic valve known. Ventral part of L1 narrow, prominent ridge which lies much lower than the ventral part of L2, and becomes obsolete at the ventral end of the speral knob. Dorsal part of L1 developed as a speral knob with poorly defined anterior and dorsal margins, merging in these directions smoothly into the surface of the valve. The top of the speral knob is situated at its dorsal end, and lies at about the same level as the top of L3. The dorsal end of the knob reaches the dorsal margin of the valve. Ventrally the ventral part of L1 is continuous with the histial ridge. Ventral part of L2 broad, decreasing in width dorsally, dorsal part of L2 narrow, tapering dorsally and becoming obsolete at about the mid-height of the speral knob. L3 moderately broad, slightly constricted close to its ventral end, otherwise of about uniform width, highest point at about the middle of the lobe. L4 ventrally much narrower than L3, expanding posterodorsally, rather flattened. S1 narrow, moderately deep behind the speral knob, shallow but distinct ventrally of the knob and behind the ventral ridge-like part of L1. S2 and S3 of about equal width, S2 perhaps somewhat wider and deeper than S3, slightly expanding in its middle part.

Histial ridge moderately broad (tr.), with a concave lateral surface, merging dorsally with only a faint change in convexity into the ventral end of L2, and separated from that of L3 by a poorly defined furrow. In posterior direction the histial ridge merges into the general surface of the valve a bit ventrally of the mid-height of the valve, and at about the transversal line through the middle of L4. A distinct velar ridge is present, but the details of its extension could not be observed.

The whole surface of the domicilium except for the bottom of S2 ornamented by a minute reticulation. The histial flange covered with distinct minute concentric striae.

Dimensions.—Length of the valve 1.37 mm; height of the valve 0.79 mm.

Discussion.—Hessland (1949, p. 297, footnote) pointed out that the specimen figured by Thorslund (1940, Pl. 3, Fig. 13) as *Ceratopsis obliquejugata* and refigured herein is not conspecific with *Ceratopsis schmidti* Bonn. (= *S. obliquejugata*). The present writer agrees with Hessland in this respect. The specimen described above as *Sigmoopsis* sp. A evidently belongs to a new species, but for a proper definition of the species more material is needed. It is more similar to *S. platyceras* than to any other species of *Sigmoopsis* described so far. In the former species, however, the speral knob is delimited posteriorly and ventrally by S1, and the top of the knob lies at a lower level. Neither do the specimens of *S. platyceras* examined show any distinct trace of ornamentation.

Occurrence.—Södermanland, Tvären area, Ringsö. A boulder of the lowermost *Ludibundus* limestone.

Sigmoopsis sp. B

Pl. XI, Fig. 10.

Description.—Speral knob rounded, comparatively small, not quite reaching the dorsal margin of the valve, with transversally ovate cross-section, defined ventrally by a faint change in convexity. Lateral surface convex, poorly defined. Ventral part of L1 developed as a narrow, faint ridge which ends at the ventral margin of the speral knob. The top of the speral knob lies but slightly higher than that of L3. Ventral part of L2 expanded, decreasing in width dorsally, dorsal part narrow, curved, becoming obsolete somewhat dorsally of the mid-height of the knob. L3 moderately broad, constricted at its mid-height, ventral part expanded, highest convexity at about the ventral $^3/_5$ of the length (tr.) of the lobe. L4 rather flattened, except close to the anterior margin of its ventral part which is conspicuously elevated. S1 narrow and shallow behind the speral knob, obsolete ventrally of the knob. S2 expanding at about its mid-height, moderately deep and wide. S3 narrow and fairly shallow.

Only heteromorphs known. Dolonal flange as in *S. bergsbrunnae*, development of the velar structure not accessible for observation.

Lateral surface of the lobes ornamented with coarse pits which are somewhat smaller than those of *S. bergsbrunnae*.

Dimensions.—The specimen figured on Pl. XI, Fig. 10 has the following dimensions: length of the valve 1.23 mm; height of the valve 0.80 mm.

Discussion.—*Sigmoopsis* sp. B resembles *S. bergsbrunnae* as well as *S. perpunctata*. It differs from both species by a somewhat larger size of the hetero-

morphs, feebly developed ventral part of L1, obsolescence of S1 ventrally of the speral knob, and by the narrow S3. From *S. perpunctata* it differs furthermore by the absence of smooth borders around the lateral surface of the lobes, and from *S. bergsbrunnae* by a lower and rounded speral knob. The specimens described evidently belong to a new species, but more material is needed in order to give this species a proper characterization.

Occurrence.—*Crassicauda* beds. Västergötland, Stora Åsbotorp bore (2 heterom.).

Gen. *Polyceratella* Öpik, 1937

Type Species.—*Ulrichia kuckersiana* Bonnema, 1909.

Diagnosis.—Quadrilobate, L1 and L4 directed more or less parallel to the anterior and posterior margin of the valve, respectively, connected ventrally by a connecting lobe. L3 constricted ventrally and expanded dorsally, ventral end confluent with the connecting lobe or separated from it by a furrow. L2 knob-like, separated from the connecting lobe by a furrow or almost obsolete. S2 long, narrow ventrally and expanding dorsally. Tecnomorphs with a histial ridge, heteromorphs with a flange-like histial dolon, broadest anteroventrally and protruding considerably in ventral direction. The lateral surface of the histial structure merges into that of the lobes without any external boundary. A ridge- or flange-like velar structure invariably present.

Species.—*Ulrichia kuckersiana* Bonnema, 1909
Polyceratella tetraceras Öpik, 1937
Polyceratella bonnemai Thorslund, 1940
Ceratopsis bicornis Neckaja, 1953.

Generic Characters.—Outline strongly preplete. L1 and L4 comparatively narrow, their outer margin more or less parallel to the anterior and posterior margin of the valve, respectively; ventrally they are connected with each other by a narrow connecting lobe. L2 usually knob-like, separated from adjacent lobes by a shallow furrow. In *P. tetraceras* it is almost obsolete. L3 narrow ventrally, strongly expanding posterodorsally, flattened, roughly fan-shaped, its ventral end continuous with the connecting lobe, or separated from the latter by a shallow furrow. Dorsal ends of L1 and L4 bulbous in some species. S1 and S3 run more or less parallel to the margin of the valve, have mostly more or less uniform width along their whole extension or taper slightly in ventral direction. S2 expanding in dorsal direction, broader than the other sulci.

Only in *P. kuckersiana* both dimorphs are known so far; from other species only tecnomorphs have been found. Tecnomorphs with a wedge-like histial ridge which continues as a sharp edge along the external margin of the lateral surface of L4 and, except of *P. bonnemai*, also as a similar edge on L1. Hetero-

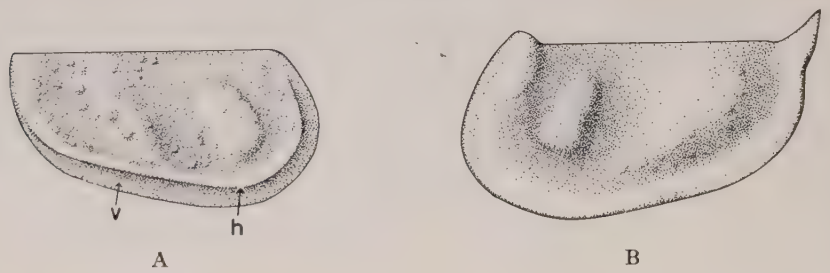


Fig. 42. Reconstructions of (A) a tecnomorph of *Polyceratella bonnemai* (THORSL.) after the holotype and (B) of a heteromorph of *P. kuckersiana* (BONN.) after the specimen figured on Pl. XI, Figs. 13–14. Note the broad velar flange (*v*) in *P. bonnemai*. *h*, histial ridge. ×35.

morphs with a moderately broad, flange-like histial dolon, broadest anteroventrally and protruding considerably beyond the free margin (Pl. XI, Figs. 13–14). The lateral surface of the histial structure merges smoothly into that of the lobes, and in lateral view the real boundary between the lobes and the histium is visible usually first on immersion of the specimen into some liquid.

A velar structure is invariably present. It may be developed as a velar ridge as in *P. kuckersiana* (BONNEMA 1909, Pl. VI, Fig. 14) or as a moderately broad velar flange as in *P. bonnemai* (Text-fig. 42 A, Pl. XI, Fig. 11). Regarding the closure of the carapace cf. BONNEMA (1909, p. 52).

DISCUSSION.—The presence of a typical histial dimorphism shows conclusively that *Polyceratella* is a sigmoopsid genus. Also the general appearance of the lobation resembles that of other quadrilobate sigmoopsids. *Polyceratella* clearly differs from all other genera of this family by its characteristic pattern of lobation and the posterior extension of the histial structure. Its relationship within *Sigmoopsidae* is not quite clear so far, but it may be close to certain velate genera as *Sigmoopsis*.

OCCURRENCE.—*Polyceratella* has been recorded from the Uhaku and Kukruse Stages of Estonia and from the *Ludibundus* limestone of Sweden.

Polyceratella kuckersiana (BONNEMA, 1909)

Pl. XI, Figs. 13–15; Text-fig. 42B.

1909 *Ulrichia Kuckersiana* n.sp.—BONNEMA, pp. 51–53, Pl. VI, Figs. 10–15.
1934 *Ulrichia kuckersiana* BONNEMA—BASSLER & KELLETT, p. 490.
1937 *Polyceratella kuckersiana* (BONNEMA)—ÖPIK, p. 37.
1955 *Polyceratella kuckersiana* (BONNEMA)—SARV, p. 15.
1956 a *Polyceratella kuckersiana* (BONNEMA)—SARV, p. 50.

LECTOTYPE (designated herein).—Tecnomorphic carapace, TM no. Os-2193, figured by BONNEMA 1909, Pl. VI, Figs. 10–14.

TYPE LOCALITY.—Kukruse, Estonia.

TYPE STRATUM.—Kukruse Stage, probably its lower zone ($C_{II}\alpha$).

DIAGNOSIS.—Length of the heteromorphs 1.25–1.30 mm. Dorsal part of L1 and of L4 expanded, bulb-shaped, their dorsal end pointed and slightly protruding beyond the hinge-line. L2 broad, expanding dorsally. L2 and L3 ornamented by a small number of low, poorly defined tubercles.

MATERIAL.—1 tecnomorph and 2 heteromorphs from Öland, 9 tecnomorphic valves from C_{II} of Estonia.

DESCRIPTION of the material from Öland.—Dorsal part of L1 bulbous, with a strongly convex posterior margin, highest at its dorsal end, pointed, protruding in laterodorsal direction, dorsal end reaching slightly beyond the hinge-line. Anterodorsal margin of L1 more or less straight, bearing a sharp edge, protruding anteriorly almost beyond the free edge. The edge extends dorsally up to the dorsal end of L1, and continues ventrally into the histial ridge. L2 forms a large, low knob, highest dorsally at a point which apparently corresponds to the preadductorial node, sloping rather steeply in dorsal and posterior, and more gently in ventral direction. L3 flattened, expanding in posterodorsal direction, the ventral part separated from the histium by a slight change in convexity; dorsally L3 becomes almost obsolete before reaching the dorsal margin of the valve. Dorsal part of L4 somewhat expanded, forming a broad, posterodorsally directed spine; posterior margin of L4 slightly protruding beyond the free edge, bearing a sharp edge which is ventrally continuous with the histial ridge. S1 rather shallow, dorsal part posterodorsally directed, ventral part curved posteroventrally and continuous with the faint depression which separates L2 from the connecting lobe. S2 broadest anteriorly, fairly shallow, decreasing in width anteroventrally. S3 deepest posteroventrally, becoming obsolete dorsally at about the height of the ventral end of the bulbous part of L4. The dorsal ends of L1 and L4 lie highest, that of L1 slightly higher than that of L4. The top of L2 lies at a considerably higher level than that of L3.

The lateral surface of the valve is surrounded along the free margin by a histial structure which can be said to run uninterruptedly from the dorsal end of L1 to that of L4. Anteriorly and posteriorly the histial structure forms in both dimorphs a faint ridge, or, rather, a sharp edge. In tecnomorphs the histial ridge is ventrally narrow and of an almost uniform width, being only slightly broader than anteriorly and posteriorly. In the heteromorphs the histium forms a moderately broad dolonal flange, along the ventral and anteroventral margin of the valve, protruding considerably beyond the free edge. It is broadest anteroventrally. The tecnomorphic histial ridge runs more or less parallel to the free edge, whereas in the heteromorphs the histial flange is slightly curved anteroventrally towards the free margin. The inner limit of the histium is not discernible on the lateral surface of the valve, the surface of the histium merging continuously into that of the lobes (Pl. XI, Fig. 13). This limit becomes, however, sharp on immersion of the specimen in some liquid (Pl. XI, Fig. 14). A faint velar ridge is present, similar to that figured in this species by BONNEMA (1909).

The ornamentation consists of a small number of rather large but low and poorly defined tubercles on L2 and L3.

Dimensions.—Specimen figured on Pl. XI, Figs. 13–14: length of the valve 1.27 mm, height of the valve 0.66 mm. Left heterom. valve RM no. Ar. 20121: length 1.29 mm, height 0.66 mm.

Discussion.—The specimens from Böda Hamn, Öland, agree with the specimens from Estonia in all essential features.

Occurrence.—According to Sarv (1956a, p. 50) *Polyceratella kuckersiana* occurs in Estonia in the Uhaku ($C_I c$) and Kukruse (C_{II}) Stages. In Sweden it has been found only in the *Ludibundus* limestone in the exposure close to the beach of Böda Hamn (2 heterom.) and in the core of the Böda Hamn boring (1 tecnom.), Öland.

Polyceratella bonnemai Thorslund, 1940

Pl. XI, Figs. 11–12; Text-fig. 42A.

1940 *Polyceratella bonnemai* n.sp.—Thorslund, p. 171, Pl. 4, Fig. 11.

Holotype.—Right tecnomorphic valve, UM no. T 36, figured on Pl. XI, Figs. 11–12, Thorslund 1940, Pl. 4, Fig. 11.

Type Region.—Södermanland, Tvären area, Ringsö, boulders.

Type Stratum.—Lowermost *Ludibundus* limestone.

Diagnosis.—[Only tecnomorphic valves known.] L1 and L4 of more or less uniform width along their whole extension, their dorsal ends not bulbous and not protruding beyond the hinge-line. A distinct histial structure developed only on the posterior half of the valve. The velar structure forms a broad flange, protruding considerably beyond the free margin. Ornamentation on the whole as in *P. kuckersiana*.

Material.—The holotype is the largest specimen found, but it is not certain whether or not it represents an adult valve. In addition 6 small valves have been encountered.

Description of the Holotype.—L1 of more or less uniform width (long.), rounded, ventrally continuous with the connecting lobe, highest at about the height of the dorsal end of L2, becoming continuously lower from this point in dorsal direction, and almost obsolete before reaching the dorsal margin of the valve. L2 rather large, oblong, moderately convex, separated from the connecting lobe by a distinct furrow and thus shaped as a knob. L3 flattened, narrow anteroventrally, expanding posterodorsally, rather poorly defined. L4 comparatively low, with a sharp peripheral edge. The highest point of the valve lies at the dorsal end of L2. S1 rather shallow dorsally, deeper ventrally, continuous with the rather deep furrow which separates L2 from the connecting lobe; S2 comparatively shallow, narrow anteroventrally, expanding posterodorsally; S3 shallow.

The sharp edge at the posterior margin of the lateral surface of L4 continues in ventral direction in a narrow histial ridge which disappears ventrally of L2. The outer side of L1 is more or less rounded. In ventral view the lateral surface of the lobe connecting L1 and L3 is rather low, whereas that of the connecting lobe between L3 and L4 is situated at a higher level (Pl. XI, Fig. 12). The velar structure is developed as a comparatively broad flange, broadest posteroventrally (cf. Fig. 42 A).

The ornamentation consists of rather coarse, but low and poorly defined tubercles on the lateral surface of L2 and L3, and on the inner parts of L1 and L4. In general the tubercles are similar to those of *P. kuckersiana* which species, however, does not seem to possess any distinct tuberculation on L1 and L4.

The small valves examined are rather similar to the holotype, but L1 and L4 are as a rule lower, and the velar structure seems to be narrower.

Dimensions.—See Table 31. In measuring the length and height the ventral margin of the velar flange and that of the histial ridge have been regarded as the ventral margin of the valve and of the lateral surface of the domicilium, respectively.

Table 31.

No.	UM Mus. cat. no.	L. valve	H. valve	L. domic.	H. domic.	Valve	Remarks
1	T 36	1.27	0.63	1.19	0.57	t—r	Holotype.
2	T 268	—	—	1.03	0.53	t—r	
3	T 270	—	—	0.99	0.51	t—l	
4	T 272	—	—	0.85	0.44	t—l	
5	T 269	—	—	0.84	0.44	t—l	
6	T 271	—	—	0.68	0.38	t—l	

Discussion.—*Polyceratella bonnemai* differs from the other species of *Polyceratella* mainly by the restricted development of the tecnomorphic histial ridge, dorsally narrow L1 and L4, which do not protrude beyond the hingeline, and by the characteristically arched outer margin of the lateral surface of the valve in ventral view, conspicuous even in the smallest specimens examined.

Occurrence.—Södermanland, Tvären area, boulders. Lowermost *Ludibundus* limestone.

Gen. *Sigmobolbina* Henningsmoen, 1953

Type Species (Henningsmoen 1953a, p. 206).—*Entomis oblonga* var. *Kuckersiana* Bonnema, 1909.

Diagnosis.—Unisulcate, S2 long (tr.), broadest dorsally, tapering ventrally, sigmoidal. Ventral part of the postadductorial area of the domicilium inflated

into a posteroventral lobe. Both dimorphs with a strong velar ridge or flange. Tecnomorphs without a histial structure, heteromorphs with a flange-like histial dolon which is anteriorly confluent with the velar structure. No marginal flange.

Species.—*Entomis sigma* Krause, 1889
Entomis oblonga var. *Kuckersiana* Bonnema, 1909
Entomis variolaris Bonnema, 1909
Dilobella longocarinata Neckaja, 1953
Sigmobolbina monoceratina n. nom.
Sigmobolbina sigmoidea n. sp.
Sigmobolbina pentagona n. sp.

It is difficult to give a safe generic reference for *Sigmobolbina*-like species in which one of the dimorphs is unknown since the lateral views of *Sigmobolbina* and *Lomatobolbina* are closely similar. For this reason the *Sigmobolbina*-like species described by Krause (1891, 1892) and Steusloff (1894) from North German erratic boulders cannot at present be assigned with certainty to a genus. Such species are *Entomis sigma ornata* Krause, 1891, *Entomis obliqua* Krause, 1892, and *Entomis oblonga* Steusloff, 1894. In case the type material of these species is lost, they must apparently be regarded as nomina dubia.

Sigmobolbina monoceratina n. nom. is the new name for *Entomis obliqua* var. *kuckersiana* Bonnema, 1909 (homonymous with *Entomis oblonga* var. *kuckersiana* Bonnema, 1909). Holotype: left heteromorphic valve figured by Bonnema 1909, Pl. V, Figs. 15–16; type locality: Kukruse, Estonia; type stratum: Kukruse Stage (probably the lower zone, $C_{II}\alpha$). For description, see Bonnema 1909, pp. 66–69.

Generic Characters.—Outline of the valve as a rule distinctly preplete with a well defined posterior swing. Anteroventral part of the postadductorial area usually swollen, forming a posteroventral lobe. In *S. monoceratina* the top of the lobe is produced into a spine. Dorsum very low.

In all known species of *Sigmobolbina* the shape of the sulcus is fairly constant. It is widest dorsally, and decreases in width in ventral direction. The ventral part of the sulcus is more anteroventrally curved than the dorsal part. Its ventral end is directed transversally just before reaching the histium. Thus the sulcus describes a sigmoidal curve. A small, poorly defined preadductorial node is usually present in front of the middle of the sulcus.

Velar structure developed as a ridge or a narrow flange in both dimorphs, more or less parallel to the free edge in tecnomorphs. The latter possess no trace of a histial structure. The statement by Henningsmoen (1953a, p. 207) that the male type of this genus has a carinal (= histial) ridge is obviously due to a mistake. Heteromorphs with a moderately broad (tr.), ventral and anteroventral, flange-like histial dolon which protrudes considerably beyond the free margin. The lateral surface of the histial dolon merges smoothly into

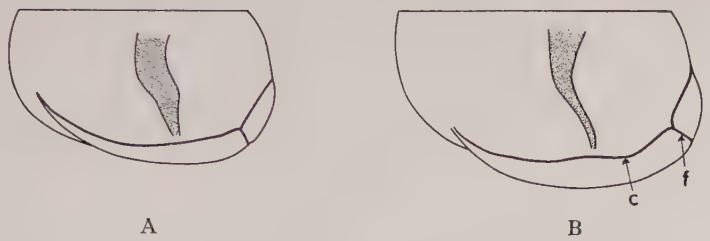


Fig. 43. Diagrammatic drawings of heteromorphs of (A) *Sigmobolbina pentagona* n.sp. and (B) *S. sigmoidea* n.sp. The contact line (*c*) between the dolon and the histium is drawn as seen on immersion of the specimen into a liquid. Note the differences between these species in the position of the line of coalescence (*f*) of the histium and the velar structure. ×40.

the lateral surface of the domicilium. On immersion of the specimens into a liquid this boundary is marked by a dark line along the contact area between the histium and the domicilium (cf. Text-fig. 43; Pl. XI, Fig. 17). In all species the dolon is anteriorly fused with the velar ridge (Pl. XII, Fig. 5), the line of coalescence being visible as a dark line on immersion of the specimens into a liquid (cf. Text-fig. 43). Anteriorly from the line of coalescence the adventral structure continues for a short distance as a moderately broad, slightly convex flange, being formed evidently by the velar structure. The anterior end of the flange curves towards the free margin, and changes into a velar ridge resembling in position and appearance that of the tecnomorphs. In posterior direction the dolon merges smoothly into the general surface of the valve.

Discussion.—The external appearance of *Sigmobolbina* resembles that of *Lomatobolbina* to such an extent that the generic reference of a *Sigmobolbina*-like species is difficult without the knowledge of the development of the adventral and marginal structures. *Sigmobolbina* differs from *Lomatobolbina* mainly by the two following characters: (1) the tecnomorphs lack a histial structure, but possess a distinct velar structure; (2) no marginal flange is developed. These two genera and *Oecematobolbina* are evidently closely related. At present there is no evidence to suggest that these unisulcate genera have originated from some quadrilobate ancestor by obsolescence of the lobes and S1 and S3.

Occurrence.—The vertical distribution of *Sigmobolbina* is incompletely known. The earliest *Sigmobolbina*-like forms occur in Sweden in the *Platyurus* limestone, but their generic reference is still uncertain. Sarv (1955, p. 16) recorded a species of *Sigmobolbina* from the *Lepidurus* limestone ($B_{II}\gamma$) of Estonia, but this species may belong to *Aulacopsis* or to some other genus not distinguished by him. According to him a member of this genus is common in the Upper Ordovician (F_1a–F_1c) of Estonia, but also in this case the generic reference needs further confirmation. In Scandinavia no species with certainty referable to *Sigmobolbina* is known from the Upper Ordovician. Outside Baltoscandia this genus has not been recorded.

Sigmobolbina sigmoidea n. sp.

Pl. XI, Figs. 16–20; Text-fig. 43 B.

Holotype.—Left heteromorphic valve (SGU), figured on Pl. XI, Figs. 16–18.

Type Locality.—Öland, Gammalsby bore.

Type Stratum.—*Crassicauda* limestone, at the level of 1.40 m of the core.

Derivation of the Name.—*sigma*-like, referring to the shape of the sulcus.

Diagnosis.—Length of the heteromorphs 0.98–1.15 mm. Tecnomorphic valves comparatively long, with a narrow velar ridge. Ventral part of the sulcus narrow and deep. The line of coalescence between the histium and the velum situated at about the longitudinal line through the middle of the ventral part of the sulcus. Surface of the domicilium smooth or almost smooth.

Description.—Tecnomorphs comparatively long and narrow (tr.). Preadductorial area moderately convex, ventral part of the postadductorial area inflated, forming a conspicuous, broad, rounded posteroventral lobe which protrudes slightly in ventral direction. The surface of the lobe merges smoothly into the dorsal part of the postadductorial area. Highest convexity of the valve somewhat in front of the mid-length of the postadductorial area and slightly ventrally of the mid-height of the valve. Sulcus distinctly sigmoidal, with a moderately broad dorsal, and a narrow and deep ventral part which in heteromorphs is distinct up to the histium.

Tecnomorphs with a narrow, edge-like velar ridge (Pl. XI, Fig. 20), situated fairly close to the free edge. Heteromorphs ventrally and anteroventrally with a moderately broad, faintly convex, flange-like histial dolon. The lateral surface of the dolonal flange merges into that of the domicilium without any distinct boundary or is separated from it by only a faint change in convexity. Anteriorly the dolonal flange coalesces with the velar ridge at about the longitudinal line through the middle of the ventral part of the sulcus (cf. Fig. 43 B). The posterior end of the dolon merges into the general surface of the valve somewhat ventrally of the mid-height of the postadductorial area. In front of the line of coalescence the velar structure continues as a narrow, faintly convex velar flange the anterior end of which arches towards the free margin, and continues in the velar ridge of the tecnomorphic type. The change from the velar flange to the velar ridge takes place at about the mid-height of the preadductorial area.

On most specimens examined no ornamentation of any kind could be observed on the lateral surface of the domicilium. Some specimens, however, exhibited a very faint granulation, visible only under high magnification and with strong, slanting illumination.

Dimensions.—See Table 32.

Discussion.—*Sigmobolbina sigmoidea* differs from other species of the genus mainly by the rather long and narrow (tr.) tecnomorphic valves, the narrow

Table 32.

No.	Mus. cat. no.	L. valve	H. valve	H-L	Valve	Locality	Remarks
1	SGU	1.09	0.63	0.90	h—l	Gammalsby 1.40 m	Holotype. Pl. XI, Figs. 16–18.
2	,,	1.09	0.60	—	h—r	,, 3.40 m	
3	,,	1.03	0.55	0.91	t—l	,, 3.10 m	Figured on Pl. XI, Fig. 20.
4	UM Öl.828	1.10	0.65	—	h—l	Böda Hamn 5.61 m	
5	UM Öl.504	1.13	0.66	0.96	h—l	Källa, quarry SW of the church	
6	UM Öl.827	1.08	0.59	—	h—r	,,	
7	UM B 296	1.01	0.60	—	h—r	Erken, boulder no. 10	
8	UM B 295	0.99	0.60	—	h—l	,, ,, ,, ,,	

and deep ventral part of the sulcus, and the smooth or nearly smooth lateral surface of the domicilium. *Entomis sigma* KRAUSE (1889, Pl. I, Figs. 11–12) exhibits on the whole a rather close similarity to *S. sigmoidea*. KRAUSE's figures, however, show much wider (tr.) valves with a rather evenly rounded outline, and a narrow dorsal part of the sulcus. It is doubtful whether this species is recognizable without a re-examination of the type material.

OCCURRENCE.—*Sigmobolbina sigmoidea* occurs in the *Crassicauda* limestone, and possibly also in the uppermost beds of the *Schroeteri* limestone as well as in the lowermost beds of the *Ludibundus* limestone.

Öland.—Gammalsby bore (6 heterom., 2 tecnom.); Böda Hamn bore (4 heterom.); quarry SW of the Källa church (3 heterom.). *Östergötland.*—Smedsby Gård bore (2 heterom.); Motala bore (2 heterom., 1 tecnom.). *South Bothnian area.*—Erken, boulder No. 10 (2 heterom., 3 tecnom.).

Sigmobolbina pentagona n. sp.

Pl. XII, Figs. 1–5; Text-fig. 43 A.

HOLOTYPE.—Right heteromorphic valve, UM no. T 145, figured on Pl. XII, Fig. 3.

TYPE LOCALITY.—Tväreń area, Ringsö, boulders.

TYPE STRATUM.—Lowermost *Ludibundus* limestone.

DERIVATION OF THE NAME.—Referring to the roughly pentagonal outline of the valves.

DIAGNOSIS.—Length of the heteromorphic valves 0.97–1.05 mm. Posterior margin of the valve rather broadly rounded, middle part of the ventral margin almost straight, ventral part of the sulcus broad and shallow, posteroventral lobe moderately high. Line of coalescence of the histial dolon and the velar structure situated slightly in front of the mid-length of the preadductorial area. Lateral surface of the domicilium very finely reticulate.

MATERIAL.—5 heteromorphic and 18 tecnomorphic valves.

DESCRIPTION.—Lateral outline of the valves roughly pentagonal, middle part of the ventral margin more or less straight, posterior end of the valve broadly rounded. Preadductorial area rather feebly convex, ventral part of the postadductorial area forms a moderately high posteroventral lobe which does not protrude in ventral direction in strictly lateral view. The lobe merges smoothly into the dorsal part of the postadductorial area. Highest convexity of the valve slightly posteroventrally from the central part of the sulcus, at about the anterior third of the length of the postadductorial area. Ventral part of the sulcus relatively broad and shallow.

Tecnomorphs with a conspicuous velar ridge (Pl. XII, Fig. 2). Heteromorphs anteroventrally and ventrally with a slightly convex, flange-like histial dolon, separated from the lateral surface of the valve by a faint change in convexity which in some specimens is developed as a semisulcus. Anteriorly the histial flange coalesces with the velar ridge at about or slightly in front of the mid-length of the preadductorial area. Development of the velar structure anteriorly of the line of coalescence as in *S. sigmoidea*. The change from the velar flange to the velar ridge takes place slightly ventrally of the mid-height of the preadductorial area. Posteriorly the histial structure is bend-like upon the dorsal half of the valve and can be followed almost up to the dorsal margin. Both valves appear to be provided with a narrow marginal ridge. Actual closure of the carapace not accessible for observation.

Lateral surface of the valve very finely reticulate. The reticulation is so faint that it does not appear on the photographs at a magnification of ×30; it is, nevertheless, present on all specimens examined. No trace of a granulation has been observed.

DIMENSIONS.—See Table 33.

DISCUSSION.—*Sigmobolbina pentagona* n.sp. differs clearly from other species of the genus, particularly by its broad ventral part of the sulcus and the orna-

Table 33.

No.	UM Mus. cat. no.	L. valve	H. valve	H-L	Valve	Remarks
1	T 145	1.04	0.53	0.86	h—r	Holotype. Pl. XII, Fig. 3.
2	T 162	0.99	0.53	0.85	h—l	
3	T 160	1.01	0.55	0.86	t—l	
4	T 161	0.99	0.56	0.86	t—r	
5	T 157	0.98	0.54	0.81	t—l	
6	T 156	0.97	0.53	0.79	t—r	
7	T 163	0.91	0.52	0.75	t—c	
8	T 146	0.87	0.50	—	t—r	Figured on Pl. XII, Figs. 1–2.
9	T 158	0.59	0.36	0.49	t—l	
10	T 159	0.46	0.29	—	t—r	

mentation. It is more similar to *S. kuckersiana* than to other species of the genus, especially in the outline of the valve. The heteromorphs of *S. kuckersiana* have a smaller size, a different ornamentation, a narrower sulcus, and evidently a more anterior position of the line of coalescence between the heteromorphic velar and histial structures. *Sigmobolbina variolaris* (BONN.), in SARV's (1956a, p. 52) opinion synonymous with *Entomis oblonga* var. *kuckersiana* BONNEMA, 1909, has according to BONNEMA (1909) still coarser tubercles than the former species.

OCCURRENCE.—Södermanland, Tvären area, Ringsö. Boulders of the lowermost *Ludibundus* limestone. In these boulders *S. pentagona* is a rather common species, whereas *S. variolaris* (BONNEMA, 1909) (cf. Pl. XI, Fig. 21), described by THORSLUND (1940, p. 173, Pl. 3, Figs. 15–16), seems to be rare. In addition to the specimens figured by THORSLUND only a few valves have been found.

Gen. *Lomatobolbina* n. gen.

TYPE SPECIES.—*Ctenobolbina mammillata* THORSLUND, 1940.

DERIVATION OF THE NAME.—From Greek λώμα = border + *bolbina*, alluding to the wide marginal flange.

DIAGNOSIS.—Unisulcate, S2 long (tr.), sigmoidal, its ventral end in heteromorphs reaching the histium. Ventral part of the postadductorial area inflated, forming a posteroventral lobe, often with a node or spine on its top. Tecnomorphs with a histial ridge, and with a faint velar ridge or without a velar structure. Heteromorphs with a moderately broad (tr.), flange-like histial dolon. In species with a velar structure the histial structure is posteriorly confluent with the former. Both dimorphs with a marginal flange, often radially striated, broadest posteroventrally.

SPECIES.—*Ctenobolbina mammillata* THORSLUND, 1940
Lomatobolbina craspedota n. sp.
? *Entomis oblonga* STEUSLOFF, 1894
? *Winchellatia gunnari* THORSLUND, 1948 (only heteromorphs known).

GENERIC CHARACTERS.—In the outline and the general convexity of the valves as well as in the shape of the sulcus *Lomatobolbina* is on the whole closely similar to *Sigmobolbina*. The outline of the valve tends, however, to be more rounded, and the posteroventral lobe to be higher and better defined. In the known species the top of the ventral lobe is provided with a node or spine. Preadductorial node low, poorly defined, situated in front of the geniculum. Dorsum very low, hardly present at all.

Tecnomorphs with a distinct wedge-like histial ridge. In ventral view the histial ridge describes a low arch the top of which is anteroventrally situated (cf. Pl. XII, Figs. 7, 11, 12). In anterior direction the ridge curves rather

steeply towards the free margin, and merges into the general surface of the valve before reaching the velar structure in those species in which the latter is present. In posterior direction the ridge curves gently towards the free margin, and its posterior end coalesces with the velar structure, if present. In tecnomorphs of *L. craspedota* no velar structure has been observed, in those of *L. mammillata* a faint velar ridge is present upon the subhistial field. In heteromorphs the subhistial field was accessible for observation only in *L. mammillata* and in a new, undescribed species of *Lomatobolbina* from the erratic boulders of the South Bothnian area. In these two species the velar structure is considerably broader in heteromorphs than in tecnomorphs, being almost as broad as the histial dolon, and the velar flange coalesces posteriorly with the dolonal flange. The differences in the width of the velar structure in tecnomorphs and heteromorphs suggest that also the velar structure may be subject to a dimorphic change comparable to that of the histial structure. A similar phenomenon has been described (BONNEMA 1909) in *Carinobolbina estona* (ÖPIK) (*Ctenobolbina carinata* in BONNEMA loc. cit.) which species, according to BONNEMA, does not possess any distinct tecnomorphic adventral structures, whereas the heteromorphs are provided with histial as well as with velar structure. The possible velar dimorphism in these species can, however, not be proved before the absence or weak development of the velar structure has been ascertained in tecnomorphs which unquestionably belong to the adult stage; the possibility that the tecnomorphs examined are preadult, and that the adult tecnomorphs in reality show a stronger development of the velar structure, can still not be excluded.

The species of *Lomatobolbina* are characterized by the presence of a moderately broad, plane, and in some species radially striated marginal flange or frill close to the free edge of the valve. The flange is as a rule broadest (tr.) posteroventrally, narrows anteriorly and posteriorly, and changes into a ridge before reaching the anterior cardinal corner or the posterior end of the valve. In tecnomorphs the subhistial field is fairly high and as a rule more or less concave. The closure of the carapace could not be examined as only separate valves have been found.

DISCUSSION.—The distinguishing features between *Lomatobolbina* and *Sigmobolbina* are discussed on p. 391. Another genus resembling *Lomatobolbina* is *Winchellatia* KAY, 1940. HENNINGSMOEN (1953a, p. 207) suggested that the spine on the posteroventral lobe in *Winchellatia* is probably a carinal (=histial) structure. As the adventral flange of this genus is situated ventrally of the spine, the flange in question was regarded by him as a velar structure. HENNINGSMOEN evidently arrived at the conclusion of the histial origin of the spine of *Winchellatia* by comparing the latter genus with *Sigmobolbina monoceratina* n.nom. In this species the spine on the posteroventral lobe forms the posterior end of the histial dolon (cf. BONNEMA 1909, Pl. V, Fig. 16), and seems, therefore, to be a part of the histial structure, whereas the velar flange is situated

ventrally of the spine and of the histial flange. HENNINGSMOEN assumed that in *Winchellatia* the histial flange, if it were present, would take the same position in respect to the spine as in *S. monoceratina*. Since the adventral flange in *Winchellatia* occupies a position resembling that of the velar structure in *S. monoceratina* this flange was regarded by him as a velar structure. In the described species of *Lomatobolbina* also the histial structure is situated ventrally of the spine on the posteroventral lobe (cf. Pl. XII, Figs. 7, 11, 12), and in this case the spine can evidently not be regarded as a part of the histial structure. There is thus no real evidence suggesting that the spine in *Winchellatia* is of histial, and its dimorphic adventral flange of velar origin. According to KAY's illustrations of *Winchellatia longispina* (KAY 1940, Pl. 32, Figs. 1–5) the adventral dimorphic flange of this species is closely similar to the histial structure in *Lomatobolbina*, and seems likewise to be of histial origin. In this species the lateral surface of the dolon merges smoothly into that of the domicilium (cf. KAY 1940, Pl. 32, Figs. 1, 3) as is the case in almost all sigmoopsids. Also other features of the valve of *Winchellatia*, such as the strongly preplete outline, the presence of a posteroventral lobe, and the general shape of the sulcus suggest sigmoopsid affinities. In the present paper *Winchellatia* is regarded as a sigmoopsid genus without a velar structure and with a histial dimorphism.

Winchellatia differs from *Lomatobolbina* by the following characters: (1) The sulcus is much shorter and not sigmoidal; (2) no velar structure is present even in heteromorphs; (3) a marginal flange is missing.

OCCURRENCE.—The earliest known species of *Lomatobolbina* occur in the *Crassicauda* limestone. Also some Upper Ordovician species (as for instance *Sigmobolbina*? sp. HENNINGSMOEN 1954b, p. 77) may belong to this genus, but, being incompletely known, their generic reference cannot be proved so far.

Lomatobolbina mammillata (THORSLUND, 1940)

Pl. XII, Figs. 6–8.

1940 *Ctenobolbina mammillata* n.sp.—THORSLUND, p. 174, Pl. 2, Figs. 8–9.
1953 a *Sigmobolbina*? *mammillata* (THORSLUND)—HENNINGSMOEN, pp. 207–208.

HOLOTYPE.—Left tecnomorphic valve (SGU), figured by THORSLUND 1940, Pl. 2, Figs. 8–9.

TYPE LOCALITY.—Exposure 1.2 km W of Tandsbyn railway station, Brunflo-Lockne area, Jämtland.

TYPE STRATUM.—Lowermost *Ludibundus* limestone.

DIAGNOSIS.—Length of the heteromorphs about 1.40 mm. Posteroventral lobe high, well defined, bearing on its top a more or less laterally directed node or spine. Tecnomorphs with a well-defined, narrow histial ridge. Both dimorphs

with a velar structure. Marginal flange narrow. Domicilium ornamented with minute granules, arranged in rows giving the ornamentation a minutely lineate or reticulate appearance.

Material.—1 heteromorphic, 5 tecnomorphic valves.

Description.—Outline preplete, ventral margin of the tecnomorphs evenly rounded, posterior swing poorly developed. Dorsal part of the preadductorial area flattened, ventral part moderately convex, highest convexity at about the longitudinal line through the spine. Ventral part of the postadductorial area inflated, forming a high, conical posteroventral lobe the top of which bears a node or short spine, pointing in lateral direction. The top of the node or spine is broken off in all specimens examined. The lobe slopes rather steeply in anterior, dorsal, and ventral but more gently in posterodorsal direction. The dorsal and posterior limit of the lobe is formed by a faint semisulcus-like change in convexity. Sulcus distinctly sigmoidal, comparatively narrow, its dorsal part rather shallow. A small, low, smooth, and fairly well-defined preadductorial node is situated in front of the geniculum.

Tecnomorphs with a narrow, distinct histial ridge. In ventral view (Pl. XII, Fig. 7) the ridge is most prominent slightly in front of the ventral end of the sulcus. Posteriorly from this point the ridge slopes gently towards the velar structure, and reaches the velar ridge slightly behind the transversal line through the posterior end of the posteroventral lobe. In anterior direction the histial ridge slopes rather steeply towards the velar ridge, and merges into the general surface of the valve somewhat ventrally of the anterior cardinal corner. Velar ridge narrow, thin, situated close to the free margin and running parallel to the latter (Pl. XII, Fig. 7). In posterior direction the velar ridge coalesces with the histial ridge slightly behind the transversal line through the posterior end of the posteroventral lobe, and as a rounded bend-like structure continues in dorsal direction from this point almost up to the posterior cardinal corner.

Heteromorphs with a prominent, moderately broad, anteroventrally flange-like histial dolon, strongly protruding in ventral direction. Its lateral surface merges with only a faint change in convexity into that of the domicilium. The anterior end of the dolon is truncated and arched towards the velar ridge, merging into the general surface of the domicilium at about the mid-height of the lateral surface of the domicilium. The posterior end of the dolon coalesces with the velar structure, the point of coalescence having the same position as in the tecnomorphs.

The examined heteromorphic valve has a moderately wide, thin velar flange of about the same width as the histial dolon. The flange is thus considerably broader (tr.) than the ridge-like velar structure of the tecnomorphs. Marginal flange narrow, situated close to the free edge. The shape and extension of this flange could not be observed in the specimens studied. The closure of the carapace was not accessible for observation.

Lateral surface of the domicilium and the subhistial field ornamented with a minute granulation. The granules are arranged in rows, and give the ornamentation a minutely lineate or reticulate appearance.

DIMENSIONS.—*a* heteromorph, figured on Pl. XII, Fig. 8; *b* tecnom., figured on Pl. XII, Figs. 6–7.

	a	*b*
Length of the valve	1.40	1.26
Height of the valve	~0.83	0.70
Length of the hinge-line	—	1.00

DISCUSSION.—*Lomatobolbina mammillata* (THORSL.) clearly differs from all other species of this genus by the shape of the posteroventral lobe, the presence of a velar ridge in tecnomorphs, and by its ornamentation.

OCCURRENCE.—Found only in the type stratum at the type locality.

Lomatobolbina craspedota n. sp.

Pl. XII, Figs. 9–12.

1940 *Ctenobolbina obliqua* (KRAUSE)—THORSLUND, pp. 173–174, Pl. 1, Figs. 21–23.

HOLOTYPE.—Left heteromorphic valve UM no. T 148, figured on Pl. XII, Fig. 9.

TYPE LOCALITY.—Tvären area, Ringsö, boulders.

TYPE STRATUM.—Lowermost *Ludibundus* limestone.

DERIVATION OF THE NAME.—From Greek κράσ–πεδον, border, referring to the wide marginal flange.

DIAGNOSIS.—Length of the heteromorphs about 1.10–1.15 mm. Posteroventral lobe prominent, bearing on its posterior part a short, posteriorly directed spine. Surface of the valve ornamented with a faint but distinct reticulation.

MATERIAL.—3 heteromorphic and 6 tecnomorphic valves.

DESCRIPTION.—Outline of the valve roughly quadrangular, distinctly preplete. Posterior end of the valve almost straight, posterior cardinal angle about 90°. Preadductorial area moderately convex, ventral part of the postadductorial area inflated, forming an oblong posteroventral lobe which slopes rather steeply in posterior and ventral direction. The dorsal boundary of the lobe is marked by a faint change in convexity. Posterior part of the lobe with a short, posteriorly directed spine. The highest convexity of the valve, the spine excluded, lies somewhat in front of the spine at about the anterior third of the length of the postadductorial area. Sulcus distinctly sigmoidal, wide dorsally, narrow and rather shallow ventrally. Preadductorial node moderately large.

Tecnomorphs with a wedge-like, narrow histial ridge which protrudes ventrally, and conceales the subhistial field in lateral view. In ventral view the

ridge describes an arch with its summit at the anteroventral margin of the valve (cf. Pl. XII, Figs. 11, 12); posteriorly the ridge is curved towards the free margin merging into the general surface of the valve before reaching its posterior end. In anterior direction the ridge seems to end rather abruptly at about the mid-height of the preadductorial area. No trace of a velar structure has been observed on any of the tecnomorphic valves examined.

Heteromorphs with a moderately broad, flange-like histial dolon. The dolon has evidently the same position upon the domicilium as the tecnomorphic histial ridge, except close to its anterior end where the dolon seems to be situated slightly higher up the side. At about the mid-length of the preadductorial area the anterior end of the dolon is curved rather steeply towards the free margin, ending abruptly before reaching the marginal flange. Lateral surface of the dolon with faint but distinct radial striae. The subhistial field in heteromorphs was not accessible for observation, and it could not be ascertained whether or not it possesses a velar structure.

Both valves with a moderately broad marginal flange. It is broadest (tr.) posteroventrally and decreases in width in anterior direction, changing into a marginal ridge at about the mid-length of the preadductorial area or slightly behind it. In posterodorsal direction the flange extends roughly up to the mid-height of the preadductorial area or slightly more dorsally, and continues from this point as a marginal ridge. In well-preserved specimens the marginal flange is ornamented with faint radial striae. In tecnomorphs the anteroventral part of the field between the histial ridge and the marginal flange is rather strongly concave.

The lateral surface of the domicilium and the subhistial field of all examined specimens ornamented with a faint but distinct reticulation. The ornamentation is so faint that it does not appear on the photographs at a magnification of $\times 37$.

Dimensions.—See Table 34. When measuring the length or the height of the valve the external margin of the histial structure has been regarded as the margin of the valve.

Table 34.

No.	UM Mus. cat. no.	L. valve	H. valve	H-L	Valve	Remarks
1	T 148	~1.13	0.65	—	h—l	Pl. XII, Fig. 9
2	T 150	1.11	0.56	—	t—l	
3	T 147	0.98	0.53	0.88	t—l	Pl. XII, Figs. 10–11

Discussion.—The lateral view of *L. craspedota* resembles that of *Sigmobolbina monoceratina* n.nom. which also has a posteriorly directed spine on the posterior part of the posteroventral lobe. *Sigmobolbina monoceratina* possesses, however, a distinct velar ridge, the histial dolon reaches posteriorly up to the posteroventral spine, and a marginal flange is missing.

It is impossible at present to decide whether *Entomis obliqua* KRAUSE (1892, Pl. XXII, Fig. 10) belongs to *Sigmobolbina* or to *Lomatobolbina*. In fact, this species is hardly recognizable on the basis of KRAUSE's description and illustrations alone. KRAUSE's original specimen was found in a boulder at Mugelsheim. Most of the ostracodes described from this boulder occur also in the erratic boulders of the *Macrourus* calcareous siltstone of Öland (ANDERSSON 1893). Thus this species has originally been described from a higher stratigraphic horizon than *L. craspedota*.

OCCURRENCE.—Södermanland, Tvären area, Ringsö. Boulders of the lowermost *Ludibundus* limestone.

Gen. *Oecematobolbina* n. gen.

TYPE SPECIES.—*Oecematobolbina nitens* n. sp.

DERIVATION OF THE NAME.—From Greek οἴκημα, chamber + *bolbina*.

DIAGNOSIS.—Unisulcate, sulcus broad dorsally, narrowing ventrally, its ventral end not reaching the histium. Tecnomorphs with a histial ridge, bearing in most species two ridge-like thickenings and, in some species, two rows of oblong pits or depressions. Heteromorphs differ from tecnomorphs by a broader, flange-like histial structure which is partitioned internally by radial septa into numerous wide, originally empty chambers. No velar structure. Both dimorphs as a rule with a broad, radially striated marginal frill.

SPECIES.—*Ctenobolbina ctenolopha* ÖPIK, 1937
Ctenobolbina polytropis ÖPIK, 1937
Oecematobolbina nitens n. sp.

A further species is described below as *Oecematobolbina* sp. A.

DISCUSSION.—In its general appearance *Oecematobolbina* resembles *Lomatobolbina*. Common to these two genera are the presence of a tecnomorphic histial structure, of a marginal frill, and the absence or weak development of the velar structure. *Oecematobolbina* is distinguished by its comparatively short (tr.) sulcus and the development of an internally partitioned histium. The type species of *Oecematobolbina* exhibits certain resemblance also to *Aulacopsis*, particularly in the general shape of the tecnomorphic as well as heteromorphic histial structure and in the shape of the subhistial field. Also in *Aulacopsis* the velar structure is missing or weakly developed. The latter genus, however, possesses a longer sulcus, different construction of the histium, and lacks a marginal frill.

Only in the type species of *Oecematobolbina* both supposed dimorphs have so far been found; of the other species listed above heteromorphs are unknown. The material examined contains two further new species, each represented by

some heteromorphic valves; more and better preserved specimens should, however, be studied before these species can be properly defined. A heteromorph of one of them is figured in the present paper (Pl. XII, Fig. 22).

The tecnomorphs of the type species possess a thick, apparently solid, wedge-like histial ridge with a sharp peripheral margin and with two ridge-like thickenings on its lateral surface. In *O. ctenolopha* (Öpik 1937, Pl. X, Figs. 17–18), *O. polytropis* (Öpik 1937, p. 33, Fig. 4, Pl. VIII, Fig. 7), and *O.* sp. A (Pl. XII, Figs. 20–21) the histial structure shows a weaker development, and its lateral surface is provided with two rows of pit-like depressions. These depressions remind of loculi, but have a different origin being formed upon the lateral surface of the histium and not between the histial flange and the free edge like the real loculi.

In the supposed heteromorphs of the type species the histial structure is broader than in tecnomorphs and partitioned internally by radial septa into 11–12 broad chambers; its shape is otherwise similar to that of tecnomorphs. The internal structure of the heteromorphic histial flange is visible only on immersion of the specimen into some liquid; in dry condition usually no trace of the internal partitions can be observed. The heteromorphs of other species of *Oecematobolbina* examined show an identical structure of the histium (cf. Text-fig. 44 and Pl. XII, Fig. 22). The details of the construction of the heteromorphic histium are not quite clear. The internal chambers were evidently empty during the life of the animal, and were subsequently filled by calcium carbonate from solution or by some other substance. The proximal ends of the cavities are not in communication with the domicilial cavity. Some specimens give the impression that the distal ends of the chambers within the histium open outwards, and that these chambers can be described as deep loculi-like tubes extending through most of the width (tr.) of the histium. It also seems to be possible that each histium contains two rows of such tubes, separated by a thin layer of shell. In this case the rows of depressions upon the histium in tecnomorphs of some species may correspond to the proximal ends of the tubes in the dolon. No complete certainty in these details of the construction of the dolon of *Oecematobolbina* can be obtained before more numerous heteromorphic specimens are available. The present information seems to suggest that the internal partitions themselves are not a dimorphic feature, but can be regarded as ventral prolongations of the depressions which in some species are present on the external surface of the tecnomorphic histial structure. In this case the function of the chambers within the dolon may have been identical with that of the internal partitions of eurychilinids and *Oepikium*, i.e. to diminish the weight of the thick histial flange and to make it stiffer mechanically.

Occurrence.—The earliest known species of *Oecematobolbina* occur in the Uhaku Stage of Estonia (Upper Llandeilian). The latest known member of this genus is a new species which occurs in the Red Tretaspis mudstones

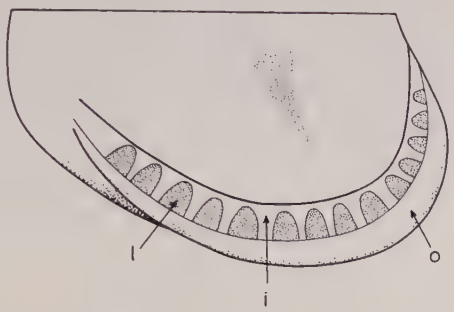


Fig. 44. Diagrammatic drawing of a heteromorph of *Oecematobolbina* sp. to illustrate the construction of the histial dolon. The dolon is drawn as seen on immersion of the specimen into a liquid. *l*, loculi-like internal cavities within the lateral part of the dolon; *i*, radial septa of the shell between these cavities; *o*, outer part of the histium. The development of the cavities in the outer part of the histium could not be clearly observed. After the specimen figured on Pl. XII, Fig. 22.

(z. of *Dicellogr. complanatus*) of Västergötland, Sweden. Outside Baltoscandia a species of *Oecematobolbina* has, according to information received from Dr. G. Henningsmoen, been found in Ireland.

Oecematobolbina nitens n. sp.

Pl. XII, Figs. 13–19.

Holotype.—Left heteromorphic valve, UM no. T 267, figured on Pl. XII, Fig. 14.

Type Locality.—Södermanland, Tvären area, Ringsö, boulders.

Type Stratum.—Lowermost *Ludibundus* limestone.

Derivation of the Name.—From Lat. *nitens*, shining, referring to the smooth, shiny surface of the lateral surface of the domicilium.

Diagnosis.—Posteroventral lobe very low, poorly defined, ventral part of the sulcus shallow. Tecnomorphs with a prominent, wedge-like histial ridge bearing upon its lateral surface two ridge-like thickenings. In supposed heteromorphs the histium is broader, reaches anteriorly up to the longitudinal line through the preadductorial node, and is partitioned internally into 11–12 chambers. Lateral surface of the domicilium smooth to minutely pitted.

Material.—3 heteromorphic and 9 tecnomorphic valves.

Description.—Outline distinctly preplete with a rather well-developed posterior swing. Lateral surface of the domicilium flattened. Posterior part of the preadductorial area slightly elevated, preadductorial node fairly large and prominent, its top forming the highest point of the preadductorial area. Ventral part of the postadductorial area faintly elevated, forming a low and poorly defined, scarcely distinguishable posteroventral lobe, its top lying at about the same level as that of the preadductorial node, or only slightly higher. Sulcus rather shallow, slightly constricted in the middle, ventral part formed by a shallow and ventrally ill defined depression.

Tecnomorphs with a rather thick, wedge-like, anteroventral histial structure with a sharp peripheral edge. The lateral surface of the histial ridge is more or less plane and provided with two distinct concentric ridge-like thickenings. In ventral view the histial ridge describes a low arch with its highest point at about the ventral end of the sulcus or slightly behind it. The ridge reaches anteriorly up to about the mid-height of the lateral surface of the domicilium. No trace of a velar structure. Subhistial field strongly concave along its entire extension.

In the supposed heteromorphs the histial structure is broader than in tecnomorphs, and reaches anteriorly up to the longitudinal line through the preadductorial node, but has otherwise the same general shape as in tecnomorphs. On immersion of the specimen into some liquid 11–12 broad internal cavities separated by narrow radial septa are visible within the histium. The general appearance of the internal cavities is identical with that illustrated in Text-fig. 44. The details of the construction of the histium could not be observed, the differences in the colour between the shell and the calcite filling the chambers being too slight. It is not quite excluded that also large tecnomorphs exhibit a similar structure of the histium; such specimens were rare, and the internal structure of their histial ridge could not be clearly observed.

Both dimorphs with a marginal flange which is broadest posteroventrally. Posteriorly the flange changes into a ridge at the mid-height of the postadductorial area or slightly farther in dorsal direction; anteriorly the corresponding change seems to take place slightly in front of the mid-length of the preadductorial area. The marginal flange has a rather coarse radial striation, formed evidently by a row of spines webbed together by a thin layer of shell. The distance between the individual spines is about equal to or only slightly larger than the width of the spines.

In well-preserved specimens the surface of the valve is at first sight quite smooth and shiny. A closer examination under high magnification reveals, however, very minute, closely spaced pits spread all over the lateral surface of the domicilium except for the bottom of the sulcus.

Dimensions.—See Table 35. When measuring the length and height of the valve the peripheral margin of the histial structure has been regarded as the margin of the valve.

Table 35.

No.	UM Mus. cat. no.	L. valve	H. valve	H-L	Valve	Remarks
1	T 267	1.03	0.57	—	h—l	Holotype. Pl. XII, Fig. 14.
2	T 155	0.99	—	0.93	h—l	Pl. XII, Fig. 13.
3	T 266	0.86	0.44	0.70	t—r	Pl. XII, Fig. 15.
4	T 153	0.69	0.36	—	t—r	Pl. XII, Figs. 18–19.
5	T 154	0.68	0.37	—	t—r	

Discussion.—The species described is fairly similar to *O. polytropis* (Öpik), but differs by a more prominent tecnomorphic histial ridge, shallower sulcus, more prominent preadductorial node, and other characters.

Occurrence.—Södermanland, Tvären area, Ringsö, boulders of the lowermost *Ludibundus* limestone.

Oecematobolbina sp. A

Pl. XII, Figs. 20–21.

Description.—Only one tecnomorphic valve has been found. Outline preplete, roughly quadrangular, anterior margin straight, posterior faintly curved, ventral margin more or less evenly convex. Preadductorial area flattened, anteroventral part of the postadductorial area swollen forming a poorly defined posteroventral lobe. The top of the lobe lies at about the mid-length of the valve, and forms its highest point. In posterodorsal direction the surface of the lobe merges smoothly into that of the dorsal part of the postadductorial area, ventrally the lobe slopes rather steeply towards the histium. Sulcus broad and moderately deep dorsally, narrow and comparatively deep ventrally, sigmoidal. Preadductorial node rather large, low.

Histial structure low, extending anteriorly almost to the mid-height of the preadductorial area, and posteriorly to about the posterior third of the length of the postadductorial area. Anteroventrally the histium projects slightly beyond the subhistial field, ventrally it is low, and in lateral view does not conceal the subhistial field. The lateral surface of the histium is delimited by two low ridges. The surface between the ridges carries two rows of narrow, oblong depressions, 8–10 in each row. No velar structure. Subhistial field comparatively high, slightly concave. Marginal area of the valve depressed, forming a narrow marginal flange, broadest posteroventrally, and developed as a ridge anteriorly and posterodorsally.

The lateral surface of the domicilium, the subhistial field, and the marginal flange ornamented with a distinct, rather coarse reticulation, arranged in rows which are directed transversally on the posterior part, anterodorsally on the anterodorsal part, and anteroventrally on the anteroventral part of the postadductorial area. In front of the sulcus these rows run on the whole in transversal direction.

Dimensions of the specimen described.—Length of the valve 1.07 mm; height of the valve 0.52 mm; length of the hinge-line 0.93 mm.

Discussion.—This species belongs to the group of species of *Oecematobolbina* characterized by the development of rows of depressions on the lateral surface of the histium. From all other species of this group *O.* sp. A. differs by its coarsely reticulate ornamentation, comparatively narrow marginal flange, and a more prominent posteroventral lobe. It certainly represents a new species,

but more specimens must be available before this species can be properly defined.

Occurrence.—Södermanland, Tvären area, Ringsö. Boulders of the lowermost *Ludibundus* limestone.

Fam. OEPIKIUMIDAE nov.

Diagnosis.—Histial frill of both dimorphs wide (tr.), partitioned internally into numerous, radially directed, narrow, evidently empty chambers. Posterior margin of the frill long, straight or slightly concave. Heteromorphs with a convex histial dolon along the whole extension of the frill. No velar structure.

Discussion.—The genus *Oepikium* Agnew, 1942, is the only known member of this family. The taxonomic position of this genus has been much discussed. E. A. Schmidt (1941, pp. 33–34) stated that he was unable to settle its family membership on account of the remarkable combination of its characters. He included it provisionally in *Hollinidae* basing himself mainly upon the shape and position of the posterior margin of the frill. According to Henningsmoen (1953a, p. 219) *Oepikium* is probably related to *Ctenonotella*. He included the former genus first (1953a) in *Piretellinae* and later (1954c) in *Ctenonotellinae*. Kesling (1955a) stated that even though *Oepikium* differs greatly from the *Hollinidae* in lobation he believed it to be a hollinid. Sarv (1955, p. 20, Table 3) considered *Oepikium* to be closely related with *Dilobella* and *Sigmobolbina*.

The major point in the decision of the taxonomic position of *Oepikium* is whether its frill is velar or histial. As pointed out on p. 231 the position of the contact area between the frill and the domicilium of *Oepikium* differs distinctly from that of eurychilinids. The area between the frill and the free edge is high ventrally, and decreases considerably in width in anterior as well as in posterior direction (cf. Bonnema 1909, Pl. V, Figs. 4, 5; Öpik 1937, Pl. V, Fig. 4). The ventral end of the long and somewhat sigmoidal sulcus reaches the inner margin of the frill. In all these respects *Oepikium* agrees closely with the heteromorphs of unisulcate sigmoopsids. The high position of the frill and the close similarity in the course of the contact area between the frill and the domicilium with that of certain sigmoopsids suggests that the frill of *Oepikium* is of histial origin. This suggestion is further supported by the conspicuous resemblance between *Oepikium* and the heteromorphs of the hollinid genus *Grammolomatella*. The heteromorphs of the latter genus agree with *Oepikium* not only in the shape of the sulcus and of the subhistial field, but also in the shape and extension of the histial structure. It should be noted that the type species of *Grammolomatella* was originally described as a species of *Biflabellum* (– *Oepikium*), and that this species would probably still have been included in *Oepikium* or in a genus close to it if the tecnomorphs had been unknown. The

histial dolon of *Grammolomatella* has, however, no internal partitions, and the tecnomorphs differ considerably from those of *Oepikium* by the lack of a frill and the possession of two pairs of histial spurs.

The construction of the frill of *Oepikium* has been thoroughly discussed by KESLING (1955a). It closely resembles that of eurychilinids (cf. p. 230), being partitioned by radial septa into numerous, narrow tubules which evidently were empty during the life of the animal. In some species the frill is ornamented by a concentric striation, the striae being thickenings of shell. The specimens examined suggest that the internal cavity of the tubules is somewhat constricted at each concentric stria, giving the frill a honeycomb-like appearance in transmitted light (Pl. XIV, Fig. 4).

Oepikium differs from other hollinids by its very wide tecnomorphic frill, the width (tr.) of which may exceed the height (tr.) of the lateral surface of the domicilium, by the construction of the frill, and by the wide (tr.), strongly convex dolon.

OCCURRENCE.—See the genus *Oepikium*, p. 408.

Gen. *Oepikium* AGNEW, 1942

(= *Biflabellum* ÖPIK, 1935, non DÖDERLEIN, 1913).

TYPE SPECIES.—*Biflabellum tenerum* ÖPIK, 1935.

DIAGNOSIS.—Unisulcate, sulcus long, sigmoidal, its ventral end reaching the histium. The posterior margin of the frill is situated considerably ventrally of the posterior cardinal corner.

SPECIES.—*Entomis* (*Primitia*) *flabellifera* KRAUSE, 1892
Biflabellum tenerum ÖPIK, 1935
Biflabellum reticulatum ÖPIK, 1937
Biflabellum crista ÖPIK, 1937
Öpikium porkuniensis HENNINGSMOEN, 1954.

In addition ÖPIK (1937) included also *Biflabellum acutum* ÖPIK, 1937, in this genus, but as the extension of the frill of this species differs considerably from that of the other species of *Oepikium* it probably belongs to a new genus.

The identity of *O. flabelliferum* has been subject to some uncertainty. ÖPIK (1937) identified with this species some specimens from the uppermost Upper Ordovician Porkuni Stage (F_2) of Estonia. HENNINGSMOEN (1954b, p. 82) pointed out that the real *O. flabelliferum* has been found in an assemblage of Middle Ordovician species, and that *O. tenerum* may be a junior synonym. For the species from F_2 figured by ÖPIK (1937, Pl. V, Fig. 8) the name *O. porkuniensis* was proposed by him (this was apparently overlooked by KESLING, 1955a, who stated on p. 268 that the Upper Ordovician species of *Oepikium* is

still unnamed). KRAUSE (1892) found *O. flabelliferum* in an erratic boulder together with several other ostracode species. ANDERSSON (1893) recorded the same assemblage of ostracodes in the erratic boulders of the *Macrourus* calcareous siltstone of Öland. The specimens found by him include also one heteromorphic valve of *O. flabelliferum* (RM no. Ar. 19819). An examination of this specimen has shown that it represents in all probability the real *O. flabelliferum*, and that it differs from *O. tenerum* by its considerably larger size, much wider (tr.) dolon, and other features.

OCCURRENCE.—An undescribed species of *Oepikium* occurs, according to SARV (1955), in the *Raniceps* beds ($B_{III}\beta$) of Estonia. The latest known species is *O. porkuniensis* from the uppermost Upper Ordovician. The genus is so far unknown outside Baltoscandia.

Oepikium sp. A

Pl. XIV, Figs. 4–5.

DISCUSSION.—A single tecnomorphic valve of *Oepikium* has been found in the South Bothnian erratic boulder Erken No. 10. It closely resembles *O. tenerum* (ÖPIK) (cf. BONNEMA 1909, p. 70, Pl. V, Figs. 1–5; ÖPIK 1935, p. 86, Fig. 40; 1937, p. 40, Pl. V, Figs. 1–4, Pl. XIV, Fig. 12; KESLING 1955 a, pp. 268–269, Pl. I, Figs. 7a–10b), but evidently attains a much larger size. The lateral surface of the domicilium is apparently smooth and the ornamentation of the frill identical with that of *O. tenerum*. *Oepikium* sp. A seems to differ from the latter species, apart from the size, by longer and stouter marginal spines and by the presence of a small node close to the anterior cardinal corner. Without examining more material, and particularly also the heteromorphic type, this South Bothnian specimen can hardly be determined specifically at present.

It is interesting to note that the inner part of the frill of the specimen figured is distinctly convex, and forms a sausage-shaped elevation (cf. Pl. XIV, Fig. 5). A similar structure is present apparently also in the tecnomorphic specimen of *O. tenerum* figured by Öpik (1937) on Pl. V, Fig. 2, and is distinctly developed on a tecnomorphic valve of this species examined by the present writer. Also the tecnomorph depicted by BONNEMA (1909, Pl. V, Fig. 1) probably possesses an identical elevation. On the other tecnomorphs of *O. tenerum* figured (ÖPIK 1937, Pl. V, Fig. 1; KESLING 1955a, Pl. I, Fig. 9) the inner part of the frill seems to be plane. The significance of these differences in the shape of the tecnomorphic frill is not clear.

DIMENSIONS.—Length of the lateral surface of the domicilium 1.79 mm; height of the lateral surface of the domicilium 0.91 mm.

OCCURRENCE.—*Crassicauda* limestone. South Bothnian erratic boulder Erken No. 10.

Fam. HOLLINIDAE Swartz, 1936

Diagnosis.—Non-sulcate to quadrilobate. Dorsal part of L3 often bulbous, that of S3 usually more persistent than S1. No velar structure. Dimorphism common, if not universal. Tecnomorphs with an adventral flange-like extension or with one or two spurs, both structures probably of histial origin. Heteromorphs with a flange- or seldom a pouch-like, probably histial dolon. Dimorphic flange solid, without internal partitions, its posterior end more or less truncated or produced into a spine. Heteromorphs of some genera loculiferous.

Subfamilies.—*Hollininae* Swartz, 1936
Ctenoloculininae Jaanusson & Martinsson, 1956
? *Graviinae* Polenova, 1952
? *Neodrepanellinae* Zaspelova, 1952.

Discussion.—The general affinities of the hollinids are discussed on p. 376. The dimorphism of *Graviinae* and *Neodrepanellinae* is unknown so far, and for this reason the inclusion of these subfamilies in *Hollinidae* is only tentative (cf. p. 377).

Occurrence.—*Grammolomatella* is the earliest known genus with a hollinid type of adventral structures, its earliest species occurring in the uppermost Middle Ordovician. The latest representatives of *Hollinidae* are recorded from Permian strata.

Subfam. HOLLININAE Swartz, 1936

Diagnosis.—Unisulcate to quadrilobate hollinids lacking the loculi in heteromorphs. Dorsal part of L1 and L3 often bulbous, but not produced into a spine.

Genera.—*Janischewskya* Batalina, 1924
Hollina Ulrich & Bassler, 1908
Hollinella Coryell, 1928
Hanaites Pokorný, 1950
Falsipollex Kesling & McMillan, 1951
Proplectrum Kesling & McMillan, 1951
Grammolomatella nov.

The present writer agrees with Henningsmoen (1953a, p. 239) on the point that the Devonian species included in *Ctenobolbina* by Kesling & Tabor (1952, 1953) seem to constitute simple hollinids, and that a new genus should apparently be erected for their reception. In these species, as for instance in "*Ctenobolbina*" *megalia* Kesling & Tabor (1952, Pl. III, Figs. 15, 17, 18; 1953, Pl. III, Figs. 18, 20, 22, 24) the dorsal part of L3 is fairly well discernible, bulbous, and rather similar to that of other hollinids. In the present writer's

opinion also the Devonian species referred to *Winchellatia* (Kesling & Tabor 1952, 1953) are not congeneric with the Ordovician representatives of this genus as they show a trace of the dorsal part of L3 similar to that in the species of "*Ctenobolbina*" mentioned above (cf. "*Winchellatia*" *teleutacea* Kesling & Tabor, 1952, Pl. III, Figs. 20, 22; 1953, Pl. II, Fig. 32). They are evidently more closely related to the other Devonian non-loculate hollinids than to the Ordovician sigmoopsids.

Occurrence.—See fam. *Hollinidae*.

Gen. *Grammolomatella* n. gen.

Pl. XII, Figs. 23–25; Text-fig. 45.

Type Species.—*Biflabellum vestrogothicum* Henningsmoen, 1948.

Derivation of the Name.—From Greek γραμμή, line + λώμα, border, alluding to the striated dolon in the type species.

Diagnosis.—Unisulcate, S2 long (tr.), geniculate, sigmoidal, dorsal end reaching the histium in heteromorphs. No trace of L3. Tecnomorphs with a pair of histial spurs on either valve; heteromorphs with a moderately broad, anteroventral and ventral, flange-like histial dolon usually covered with a radial striation. Posterior margin of the dolon long, straight or slightly concave, posterior end pointed; surface of the dolon often conspicuously depressed ventrally of the ventral end of the sulcus.

Species.—*Biflabellum vestrogothicum* Henningsmoen, 1948
Ctenobolbina diensti Kummerow, 1924
Ctenentoma? *dubitabilis* Öpik, 1953 (including *Ctenentoma*? *unguiculata* Öpik, 1953).

Generic Characters.—Outline preplete, posterior swing rather well defined. The valves are rather regularly convex without a posteroventral lobe. Sulcus geniculate, sigmoidal, long (tr.), broad dorsally, narrowing ventrally, the ventral end extending to the histium. Preadductorial node low, poorly defined. Tecnomorphs with two prominent spurs which in some species are connected by a narrow flange. The tecnomorphic valve of the type species is figured here for the first time (Pl. XII, Figs. 24–25). Ventrally it has two stout and prominent extensions; in all specimens studied the terminations of these extensions were, however, broken off, and thus their exact shape and length could not be determined. In *Ctenentoma*? *unguiculata* Öpik (= tecnomorph of *Ctenentoma*? *dubitabilis* Öpik) the histial structure is developed as a narrow flange, both ends of which are produced into long spines (cf. Öpik 1953, Pl. XII, Fig. 124).

Heteromorphs with a moderately broad, flange- or frill-like histial dolon. In anterodorsal direction the dolon decreases continuously in width until it merges rather abruptly into the general surface of the domicilium, usually

A B

Fig. 45. *Grammolomatella vestrogothica* (HENNINGSM.). A, a tecnomorph after the specimen figured on Pl. XII, Figs. 24–25. The shape of the distal ends of the spurs uncertain. B, a heteromorph after the holotype. ×30.

somewhat dorsally from the longitudinal line through the geniculum of the sulcus. In posterior direction the dolon is of uniform size or increases slightly in width up to its posterior end. Its posterior margin is long, mostly slightly concave, and with a pointed posteroventral termination. Ventrally of the ventral end of the sulcus the surface of the dolonal flange is usually concave, forming a conspicuous, fairly large depression which is best developed in the Ordovician species of the genus. The lateral surface of the dolon is radially striated at least in the type species and in *G. diensti*. No velar structure, nor marginal flange. Actual closure of the carapace not observed. Subhistial field convex, at least in the type species.

DISCUSSION.—The shape of the sulcus as well as the general shape of the valve of *Grammolomatella* resembles that of the unisulcate sigmoopsids. There is no doubt that the dimorphic adventral structure in this genus is of histial origin as the dolonal flange is placed high up laterally, and resembles also otherwise the dolon of sigmoopsids (as for instance *Sigmobolbina* and *Lomatobolbina*, cf. especially *Lomatobolbina craspedota* n.sp., Pl. XII, Fig. 9) in every important respect.

The valves described by ÖPIK (1953) as *Ctenentoma? dubitabilis* and *Ctenentoma? unguiculata* belong in all probability to a single species, the former representing heteromorphs and the latter tecnomorphs. The differences in the shape of the histial structure between these species agree with those between the dimorphs of *Grammolomatella vestrogothica*. According to ÖPIK both species occur also in the same layers. Of *Ctenobolbina diensti* KUMMEROW only heteromorphs have been described. This species was placed by HENNINGSMOEN (1954c) into *Parabolbina*, but differs from this genus particularly by a much longer and geniculate sulcus and the different shape of the dolon in heteromorphic valves.

The presence of tecnomorphic spurs and the abrupt posterior end of the solid dolonal flange are regarded in the present paper as hollinid characteristics, and for this reason *Grammolomatella* is included in *Hollinidae*.

OCCURRENCE.—Uppermost Middle Ordovician and Upper Ordovician of Scandinavia and Silurian of Norway, England, and Australia. The earliest

known species of *Grammolomatella* was found by the present writer in rock samples from the uppermost Middle Ordovician beds (4bδ) of the Oslo region (Terneholmen, Oslo-Asker). This apparently represents a new species. *G. diensti* was reported by HENNINGSMOEN (1954c, p. 58) from the Ludlowian (9d) of the Oslo region.

Superfam. LEPERDITELLACEA ULRICH & BASSLER, 1906

[*Nom. transl.* JAANUSSON, herein (*ex Leperditellidae* ULRICH & BASSLER, 1906)].

DIAGNOSIS.—Non-sulcate to quadrilobate, small to moderately large palaeocopes with preponderantly postplete, more seldom amplete to slightly preplete outline. Adventral area of the valve occasionally inflated and forming an adventral lobe, or thickened and forming a non-dimorphic carinal bend or ridge, developed mostly as a raised border along the free margin. No velar structure and no dimorphism of the adventral structures.

FAMILIES.—*Leperditellidae* ULRICH & BASSLER, 1906
Drepanellidae ULRICH & BASSLER, 1923
Aechminidae BOUČEK, 1936.

DISCUSSION.—E. A. SCHMIDT (1941, p. 41) pointed out that the adventral ridge or swelling (*Randwulst* in E. A. SCHMIDT, loc. cit.) in *Drepanella*, *Bollia*, *Ulrichia*, and allied genera is not a true velum, but a structure of different character. HENNINGSMOEN (1953a, pp. 231–232) suggested that this structure "appears to be a carinal structure, or at the best, a fused carinal and velate structure". In spite of the above considerations the structure was termed a "velate ridge" by KESLING & HUSSEY (1953, p. 81, Fig. 1) since they did not believe that a carinal structure could be distinguished if the velar structure is missing (cf. also KESLING 1951c, p. 118).

The adventral (carinal) non-dimorphic ridge in drepanellids usually has on the whole the same position upon the domicilium as L1 + connecting lobe + L4 in quadrilobate bassleratiids and sigmoopsids. It is developed mostly as a ridge- or bend-like thickening of the shell, forming a raised border around at least part of the lateral surface of the domicilium along the free margin. In some genera of *Bolliinae* and *Ulrichiinae* the inside of the adventral ridge-like elevation seems to be concave, the elevation forming a swelling of the domicilium. It thus represents a lobal structure. Such a lobe running from one cardinal corner to the other and not continuous with L2 and L3, if developed, is in the present paper called the adventral lobe (cf. p. 190). There is no evidence suggesting that a real velar structure has been present in early leperditellaceans, but has become obsolete or fused with the carinal structure.

The position of the drepanellid adventral structure recalls more that of the histial than that of the velar structure. Yet the histial structure is developed

in quadrilobate sigmoopsids as an ornamental extension from L1 and the connecting lobe, and is commonly dimorphic, wedge- or flange-like, never forming a raised border.

The leperditellids are connected with the drepanellids by a fairly continuous morphological series. The simplest leperditellids, as *Leperditella* and *Conchoprimitia*, do not possess any adventral thickening of the shell, in *Conchoprimitia*? *conchoidea*, however, a faint, raised, bend-like carinal elevation is present. The latter species reminds of *Pyxion* and *Parenthatia* in which the border-like, rounded ridge is fairly prominent. In *Kinnekullea* the anterodorsal end of the carinal ridge is bulbous or produced into a spine, foreshadowing the conditions in *Drepanella*. The former genus may, in fact, be included in *Drepanellidae*, as also suggested by HENNINGSMOEN (1948, pp. 412–413). In the writer's opinion *Drepanella* can be characterized as a bilobate and carinate leperditellid with the anterodorsal end of the carinal ridge produced into a spine. The writer is even not quite certain of the differences between *Leperditella* and *Drepanella* being really important enough for placing these genera in separate families as these differences seem to be on the whole equal to those between non-sulcate and lobate genera within the families of most other superfamilies.

The relationship between *Drepanellinae*, *Bolliinae*, *Ulrichiinae*, and *Aechmininae* was pointed out by E. A. SCHMIDT (1941) and HENNINGSMOEN (1953a). *Aechminidae* are considered, following SWARTZ (1936), as a separate family, the other subfamilies are here tentatively included in *Drepanellidae*. This classification is probably not quite satisfactory, and further studies are needed in order to ascertain the degree of relationship between the different subfamilies here included in *Drepanellidae*.

Dimorphism of leperditellacean genera has been described on several occasions, but special studies are needed in order to ascertain whether the reported differences are due to dimorphism or merely to individual variation. For further information regarding the suggested occurrence of dimorphism in *Leperditellacea*, cf. pp. 199 and 220.

Leperditellidae are one of the earliest palaeocope families known, appearing already in the Lower Arenigian, and the other leperditellacean families and subfamilies have apparently been derived from the early non-sulcate representatives of this family, as for instance *Conchoprimitia*, by successive development of a carinal structure and lobation, or of a dorsal spine. *Leperditellacea* represent the simplest type of the palaeocope ostracodes, and in this case the simplicity is apparently original (cf. p. 223).

OCCURRENCE.—The earliest leperditellaceans (*Conchoprimitia*, *Primitiella*-like forms) appear in the Lower Arenigian. It is possible that also the Upper Tremadocian genus *Nanopsis* belongs to this superfamily. The latest leperditellaceans have been recorded from Carboniferous (Pennsylvanian) strata.

Fam. LEPERDITELLIDAE Ulrich & Bassler, 1906

Syn. *Primitiidae* Ulrich & Bassler, 1923

Diagnosis.—Non- to unisulcate. The lobation, if developed, is restricted to an elevation in front of and/or behind the sulcus or the adductor scar. Adventral area of the valve thickened in some genera, forming a carinal bend or a low, rounded carinal ridge.

Genera.—*Primitia* Jones & Holl, 1865
Schmidtella Ulrich, 1892
Leperditella Ulrich, 1897
Primitiella Ulrich, 1897
Haploprimitia Ulrich & Bassler, 1923
Eridoconcha Ulrich & Bassler, 1923
Punctaparchites Kay, 1934
Conchoprimitia Öpik, 1935
Milleratia Swartz, 1936
Paraschmidtella Swartz, 1936
Parenthatia Kay, 1940
? *Pseudulrichia* E. A. Schmidt, 1941
Pyxion Thorslund, 1948
Pinnatulites Hessland, 1949
Cryptophyllus Levinson, 1951
Coeloenellina Polenova, 1952
Zaborovia Polenova, 1952
Sinoprimitia Hou, 1953
? *Nanopsis* Henningsmoen, 1954
Parapyxion n. gen.
Craspedopyxion n. gen.

Provisionally also *Ceratocypris* Poulsen, 1934, and *Balticella* Thorslund, 1940, are included in this family. The classification of certain Upper Palaeozoic genera, like *Paraparchites* Ulrich & Bassler, 1906, *Pseudoaparchites* Kellett, 1933, *Microaparchites* Croneis & Gale, 1939, etc., is still uncertain. Henningsmoen (1953a, p. 243) included them in *Kloedeninae*, but they may represent late leperditellids.

Discussion.—*Leperditellidae* were divided by Henningsmoen (1953a) into three subfamilies: *Leperditellinae*, *Conchoprimitiinae*, and *Eridoconchinae*. *Leperditella* and *Conchoprimitia* are evidently closely related, and the differences between them are certainly not of subfamiliar value (cf. p. 418). *Eridoconcha* differs from these genera mainly by the presence of an adventral (carinal) ridge-like thickening of the shell, and a fairly deep sulcus. Other genera included by Henningsmoen in *Eridoconchinae*, as *Schmidtella* and *Cryptophyllus*,

possess neither carina nor sulcus. The two latter structures show a considerable degree of variation even within a leperditellid genus. *Conchoprimitia? conchoidea* is slightly carinate, and *Parapyxion* includes species with a deep sulcus (*P. subovata*) and with hardly any sulcal or lobal structures at all (*P. obesa*; cf. THORSLUND 1948, Pl. XX, Figs. 6, 7). The material studied suggests that the carinate genera like *Pyxion* or *Kinnekullea* and sulcate genera with a node on either side of the sulcus like *Parapyxion* have developed from early non-sulcate *Conchoprimitia*-like species, possibly along several independent phylogenetic lines. If a subdivision of *Leperditellidae* were attempted along the lines indicated by HENNINGSMOEN, several new subfamilies ought to be erected, each of them including only a few closely similar genera. This seems to be unadvisable at present. On account of the general smoothness of the valves and lack of clear diagnostic characters in most genera a much closer study is needed as regards the details of the closure, hingement, and muscle scars before a reasonably sound and natural classification of these genera can be effected. Pending such studies the family *Leperditellidae* is considered in the present paper to consist of only one subfamily.

Primitiella and *Haploprimitia* differ from the other leperditellids by their long and narrow (tr.) carapace with trapezoidal, postplete outline, and if the dimorphism described by KAY (1940) in the type species of *Primitiella* should prove to be real, these genera ought probably to be removed into a separate subfamily or family (cf. also p. 221). *Primitia*, as defined by its proposed (cf. p. 217) type species, *P. mundula* (JONES) (cf. SWARTZ 1936, Pl. 79, Figs. 5a, 5b), agrees in all essential respects with the other genera of *Leperditellidae*. For this reason the family *Primitiidae* is considered in the present paper as a junior synonym of *Leperditellidae*.

OCCURRENCE.—See *Leperditellacea*, p. 413. The classification of the Carboniferous leperditellid-like genera is still uncertain, and the latest occurrence of this family can, therefore, not be determined at present.

Gen. *Conchoprimitia* ÖPIK, 1935

Syn. *Conchoides* HESSLAND, 1949
Conchoprimites HESSLAND, 1949

TYPE SPECIES.—*Conchoprimitia gamma* ÖPIK, 1935.

DIAGNOSIS.—Non-sulcate, with a short (tr.) sulcal depression or with a similar narrow sulcus; preadductorial node distinct to obsolete, no other lobal structures. Outline more or less distinctly postplete, carapace evenly convex, without a conspicuous adventral bend or thickening. Dorsum low, epicline, highest at its middle at about the mid-length of the valve; cardinal corner fields conspicuously flattened. Left valve overlapping the right one along the free margin, its internal side with a more or less distinct groove for the reception

of the free margin of the right valve. Surface smooth, punctate or reticulate, never granulose or tuberculate. Most species attain a rather large size, up to 2–4 mm in length.

Species.—*Leperditia* (*Isochilina*) *socialis* Brögger, 1882
Primitia sulcata Krause, 1889
Isochilina? *erratica* Krause, 1891
Primitia Tolli Bonnema, 1909
? *Primitia conchoides* Hadding, 1913
Primitiella glauconitica Kummerow, 1924
Conchoprimitia gammae Öpik, 1935
Conchoprimitia leperditioides Thorslund, 1940
Conchoprimites reticulifera Hessland, 1949
Conchoides meganotifera Hessland, 1949
Conchoides levis Hessland, 1949
Conchoides circumstriata Hessland, 1949
Conchoides rugosa Hessland, 1949
Conchoides ventropunctata Hessland, 1949
Conchoides dorsodepressula Hessland, 1949
Conchoprimitia eos Henningsmoen, 1954
Conchoprimitia socialis vulgaris Henningsmoen, 1954.

Henningsmoen (1954a, p. 253) suggested that *C. gammae* may be conspecific with *C. glauconitica* as described by Öpik (1935) from $B_{II}\gamma$ of Estonia. This seems to be a likely assumption. The identity of the Estonian specimens with Kummerow's *Primitiella glauconitica* from the German erratic boulders does, on the other hand, not seem to be proved beyond doubt. *Conchoprimitia tolli integra* Öpik, 1937, *C. deminuta* Öpik, 1937, and *C. tallinnensis* Öpik, 1937, were considered by Henningsmoen (1953a, p. 254) and Sarv (1956a, p. 47) as synonyms of *C. tolli* Bonnema, 1909. *Conchoprimitia*? *inusitata* Öpik, 1937, probably belongs to a new genus (cf. also Henningsmoen 1953a, p. 254). *Conchoprimitia bröggeri* Öpik, 1939, was regarded by Henningsmoen (1954a, p. 60) as synonym of *C. socialis socialis*, and *C. hallensis* Thorslund, 1940, of *C. leperditioides* (1953a, p. 255). In the present paper also *C. elongata* Thorslund, 1940, is treated as conspecific with the latter species. Henningsmoen (1954a, pp. 60–61) suggested that *Conchoides micropunctata* Hessland, 1949, is a junior subjective synonym of *Conchoprimitia socialis socialis*. The so-called "non-leperditioid group of *Conchoides*" (Hessland, 1949) ought probably to be excluded from *Conchoprimitia*; further studies are, however, needed to answer this question. *Primitia conchoides* is in the present paper only tentatively referred to *Conchoprimitia* (cf. p. 422).

Discussion.—Hessland (1949) split the genus *Conchoprimitia* in the sense of Öpik (1937) into three genera: *Conchoprimitia* (with two concentric grooves and no sulcus), *Conchoides* (with one concentric groove and no sulcus), and

Conchoprimites (with sulcus and with or without concentric grooves). HENNINGSMOEN (1953a, pp. 252–253) pointed out that the grooves upon the valve of these forms correspond to the boundary between coherent valves of two moults, or are due to an impression left by the free edge of the valve of an earlier moult. According to him these features are of a more or less accidental nature, and cannot be used either as generic or specific characters. For this reason *Conchoides* was regarded as a synonym of *Conchoprimitia*.

HENNINGSMOEN's observations and conclusions regarding the moult retention in *Conchoprimitia* have been fully confirmed by the present writer's studies. Carapaces of a Lower Ordovician species of *Conchoprimitia* examined have shown an older instar retained on one valve, but not on the other, as in a specimen of *C. deminuta* (= *C. tolli*) figured by ÖPIK (1937, Pl. XV, Figs. 4–5) and refigured by HENNINGSMOEN (1953a, Pl. 2, Figs. 8–9). Three coherent valves occur occasionally in *C.? conchoidea* (cf. e.g. HADDING 1913, Pl. VI, Fig. 16).

The single real difference known between *Conchoprimitia* and *Conchoprimites* lies in the distinctness of the sulcal structure. HESSLAND (1949) included in the former genus species without a sulcal structure or with a faint sulcal depression (as *C. circumstriata*), and in the latter genus those with a distinct sulcus (as *C. tolli*) or with a faint sulcal depression (as *C. reticulifera* or *C. elongata*). The examination of most species of these groups has shown that no distinct boundary between these genera based only on the distinctness of the sulcal structure can be drawn. The latter feature may vary even within a species from a distinct depression to an almost obsolete condition (cf. *C. leperditioidea* below). For this reason *Conchoprimites* is regarded here as a synonym of *Conchoprimitia*. It is possible that future studies may prove necessary the splitting of this genus into two or more genera, but this should be based mainly upon other characters than the relative distinctness of the sulcal structure.

HESSLAND (1949, pp. 120–121) described and depicted in *Conchoprimitia*, in addition to the scar of the adductor muscle, also the scars probably belonging to the mandibular, antennular, and dorsal groups of muscles. In well-preserved specimens scars of the supposed mandibular and antennular muscle groups are occasionally distinguishable also in the species described in the present paper. In the latter species the traces of the scars of these muscles are, however, weak, and do not appear on the photographs published. In a species of *Conchoprimitia* from the uppermost *Vaginatum* limestone impressions which evidently correspond to the scars of the mandibular and antennular muscle groups are especially distinct, particularly upon the internal moulds. Their arrangement agrees essentially with that figured by HESSLAND (1949, Pl. II, Fig. 10). This is a further proof that the accepted orientation of the carapace of *Conchoprimitia* is correct. The species mentioned and its muscle scars will be treated in a future paper.

The general features of *Conchoprimitia* closely resemble those of *Leperditella*. The type species of the latter genus (Coryell & Schenck 1941, Fig. 1) differs from *Conchoprimitia* as well as from several other species currently referred to *Leperditella* by the shape of the dorsum which is epicline, and protrudes beyond the hinge-line posteriorly, but is low and hypocline anteriorly. The internal groove on the left valve along the free margin is present also in *Conchoprimitia*.

Occurrence.—*Conchoprimitia* is one of the earliest undoubtedly palaeocope genera known in Europe. It appears in Sweden, according to the material collected by Dr. T. Tjernvik, already in the Lower Arenigian Hunneberg Stage (zone of *Megistaspis planilimbata*). The latest species occur in the *Ludibundus* limestone and contemporaneous beds (Lower Caradocian) of Baltoscandia. The genus is so far unknown outside Baltoscandia, but some North American species currently classified as *Leperditella* may in reality belong to *Conchoprimitia*.

Conchoprimitia leperditioidea Thorslund, 1940

Pl. XV, Figs. 1–6.

1940 *Conchoprimitia leperditioides* n.sp.—Thorslund, pp. 161–162, Pl. 4, Figs. 14, 15; Pl. 5, Fig. 1.
1940 *Conchoprimitia hallensis* n.sp.—Thorslund, p. 162, Pl. 5, Figs. 2–4.
1940 *Conchoprimitia elongata* n.sp.—Thorslund, p. 162, Pl. 4, Figs. 12, 13.
1949 Conchoprimites elongata (Thorslund)—Hessland, p. 236.
1949 Conchoprimites leperditioides (Thorslund)—Hessland, p. 236.
1949 Conchoprimites hallensis (Thorslund)—Hessland, p. 236.
1953 a Conchoprimites leperditioides (Thorslund)—Henningsmoen, p. 255.
1953 a Conchoprimites elongata (Thorslund)—Henningsmoen, p. 255.

Holotype.—Carapace figured by Thorslund 1940, Pl. 4, Fig. 14 (SGU).

Type Locality.—Jämtland, Hallen.

Type Stratum.—Conglomerate of the *Ludibundus* limestone.

Diagnosis.—Sulcal depression faint to almost obsolete, presulcal node flattened, scarcely distinguishable, or obsolete. Well-preserved specimens with a faint, ovate mark of the adductor scar upon the ventral end of the sulcal depression, and with a very faint ornamentation consisting of small, shallow, closely placed pits, occasionally arranged in rows and giving the ornamentation a reticulate appearance. Some specimens with faint, rather coarse, scattered pits upon the preadductorial area.

Description.—Valves moderately and rather uniformly convex; highest convexity at about the mid-length of the valve. In some large specimens with almost obsolete sulcal depression the central area of the valve is slightly inflated, forming a shield-like, poorly defined elevation. Dorsum low, strongly epicline, highest at the middle of the hinge-line. Posterior cardinal corner field flattened, usually delimited by a faint furrow or by a distinct change in the convexity of the valve. Anterior cardinal corner field smaller than the posterior

Table 36.

No.	Mus. cat. no.	L. valve	H. valve	H-L	Ratio. L./H.	Valve	Locality	Remarks
1	SGU	2.97	2.07	—	1.43	(c) l	Hallen, Jämtl.	Thorslund 1940, Fig. 15
2	,,	2.90	2.00	1.95	1.45	(c) l	,, ,,	Holotype of *C. leperditioidea*. Thorslund 1940, Pl. 4, Fig. 14.
3	,,	2.79	1.88	1.71	1.48	(c) l	,, ,,	Holotype of *C. hallensis*. Thorslund 1940, Pl. 5, Figs. 2–4.
4	,,	2.96	1.99	1.68	1.49	(c) l	,, ,,	
5	,,	2.42	1.59	1.55	1.52	(c) l	,, ,,	
6	,,	3.17	1.99	1.95	1.58	(c) l	,, ,,	Holotype of *C. elongata*. Thorslund 1940, Pl. 4, Figs. 12–13.
7	UM Öl.833	2.87	1.94	—	1.48	l	Böda Hamn 4.76 m	
8	UM Öl.832	2.36	1.54	—	1.53	l	,, ,, 0.98 m	
9	UM Öl.831	2.50	1.58	1.53	1.58	(c) l	,, ,, 0.98 m	Figured on Pl. XV, Figs. 4–6.
10	UM Öl.830	3.01	2.02	1.93	1.49	l	Böda Hamn	
11	UM D 544	2.46	1.62	—	1.52	r	Dal., Fjäcka	Figured on Pl. XV, Figs. 1–3.

one, less distinct. Surface of the valve in most specimens with a concentric groove of varying distinctness anteriorly and posteriorly, in some specimens also ventrally; other specimens without any distinct trace of a groove. The sulcal structure varies from a distinct, though shallow, sulcal depression to a scarcely distinguishable, faint depression. Preadductorial node flattened, scarcely distinguishable, forming a faint, rounded elevation in front of the depression. In small specimens the sulcal depression and the node are always much more distinct than in large specimens. Well-preserved specimens with a faint, ovate mark of the adductor scar upon the ventral end of the sulcal depression, or, when the latter is short and faint, ventrally of it. Some well-preserved specimens, particularly those with preserved ornamentation, show in front of the adductor scar a faint trace of a scar belonging probably to the mandibular muscle group, and dorsally of the latter a small depression, which may represent a scar of the antennular muscle group.

The left valve overlaps the right one along the free margin, the overlap being most pronounced along the ventral margin and fairly faint along the anterior and posterior margin of the valve. The actual closure of the carapace was not accessible for observation.

In well-preserved specimens with a distinct sulcal depression the surface of the valve except the bottom of the depression is covered with faint, minute, shallow, scarcely visible, closely placed pits which do not appear on the photographs at a magnification of ×20. The pits are in some species arranged into rows giving the ornamentation a finely reticulate appearance. Some specimens also with faint, coarse, shallow, scattered pits upon the preadductorial area. In most specimens, especially in those with an almost obsolete sulcal depression no ornamentation has been observed. This is probably due to the slightly corroded surface of the valve.

Dimensions.—See Table 36. Ratio L./H., the ratio between the length and the height of the valve.

Discussion.—Thorslund (1940) distinguished in the *Ludibundus* limestone of Jämtland between a narrow form, *C. elongata*, and a broad form, *C. leperditioidea*. A further broad form was described by him as *C. hallensis*. Henningsmoen (1953a, p. 255) considered *C. leperditioidea* and *C. hallensis* as synonyms, and pointed out that the differences between *C. leperditioidea* and *C. elongata* may be due to dimorphism, or tectonic influences. An examination of the type material of *C. leperditioidea* and *C. hallensis* has shown that these species are undoubtedly synonyms, both showing also identical ornamentation. The holotype of *C. elongata* differs by its longer and narrower carapace, almost obsolete sulcal depression, and by the absence of any trace of ornamentation. The latter feature may, however, be due to conditions of preservation, since also most of the examined valves resembling the holotype of *C. leperditioidea* do not show any trace of pits on their surface. Among specimens with the outline of the holotype of *C. leperditioidea* the development of the sulcal depression varies within rather wide limits, the sulcus being almost completely obsolete in some specimens (e.g. in the specimen UM no. Öl. 833, No. 7 in the Table 36). The length/height-ratio of the valve varies rather considerably (cf. Table 36), the holotype of *C. elongata* and the carapace of *C. leperditioidea* figured by Thorslund (1940) on Pl. 4, Fig. 15 showing extreme values among the specimens measured. It should, however, be noted that none of the examined specimens with an almost obsolete sulcal depression shows any trace of an ornamentation; whether or not this depends exclusively on the state of preservation cannot be decided at present.

It is not quite excluded that *C. leperditioidea* and *C. elongata* represent different species, but this can not be decided on the base of the available material. Both types occur in the same beds, and frequently also on the same slab of the rock. This and the obvious presence of more or less intermediate forms make it probable that the differences fall within the limits of the individual variation of a single species. The possibility of these types representing different dimorphs has been considered, but the number of available undamaged carapaces and valves has been too small for confirming this assumption. At any rate, the separation of these types has proved to be impossible in practice,

though this may depend in part on the poor state of preservation of certain features, particularly of the ornamentation, in most of the available specimens. In the present paper *C. leperditioidea* and *C. elongata* are provisionally considered as synonyms.

Conchoprimitia leperditioidea differs from the other Middle Ordovician species of the genus by the shallow sulcal depression, the flattened and poorly defined preadductorial node, and the ornamentation.

Occurrence.—This species has been found only in the lower part of the *Ludibundus* limestone.

Jämtland (cf. Thorslund 1940). *Siljan district.*—Fjäcka (7 specim.). *South Bothnian area.*—Erratic boulder Ekeby No. 89. *Öland.*—Böda Hamn boring (15 specim.), exposure at the beach of Böda Hamn (2 specim.).

Conchoprimitia? conchoidea (Hadding, 1913)

Pl. XV, Figs. 7–11.

1913 *Primitia conchoides* n.sp.—Hadding, pp. 68–69, Pl. VI, Figs. 13–17.
1913 *Primitia Tolli* Bonnema—Hadding, pp. 67–68, Pl. VI, Figs. 10, 11.
1937 *Conchoprimitia conchoides* (Hadding)—Öpik, p. 10.
1951 *Conchoprimitia conchoides* (Hadding)—Hede, pp. 69–70, 75.
1951 *"Primitia" tolli* Hadding (non Bonnema)—Hede, pp. 69, 75.
1953 *"Primitia" tolli* Hadding—Lindström, pp. 127, 129, 131.
1953 a *Conchoprimites conchoides* (Hadding)—Henningsmoen, p. 255.

Lectotype.—A young left valve with an adherent valve of the preceding instar, LM no. LO 2513 t, figured by Hadding 1913, Pl. VI, Fig. 15, in the present paper Pl. XV, Fig. 7.

Type Stratum.—Lower part of the zone of *Nemagraptus gracilis.*

Type Locality.—Scania, Röstånga, locality No. III: 6.

Diagnosis.—Non-sulcate, well-preserved specimens with a distinct, rounded, usually slightly elevated lateral surface of the adductor scar. Dorsum low, ortho- to slightly epicline, central area of the valve fairly flattened, peripheral area sloping rather steeply in all directions, adventral area somewhat thickened forming a more or less distinct carinal bend. Moult retention common. Surface of the valve apparently without ornamentation.

Description of the specimens from Scania.—Small specimens, like the retained valve of the preceding instar of the lectotype, with an indistinct, shallow sulcal depression, larger specimens without conspicuous sulcal structures. Well-preserved valves with a distinct, rounded, somewhat elevated mark of the adductor scar upon the lateral surface dorsally of the mid-height and in front of the mid-length of the valve. The interior of the valve shows at the corresponding place a prominent, elongated boss which leaves on the internal mould a narrow, deep furrow giving the mould a unisulcate appearance. In front of the adductor scar of well-preserved specimens a shallow, indistinct,

rounded depression probably indicates the position of the muscle scar of the mandibular group; between this depression and the adductor scar the lateral surface of the valve is often slightly elevated; also the area in front of the supposed mandibular depression is usually somewhat inflated.

Dorsum narrow (tr.), orthocline to faintly epicline, merging in ventral direction more or less smoothly into the surface of the valve. Central area of the valve in most specimens comparatively weakly convex, surrounded along the free margin by a more or less distinct bend which is formed by a thickening of the shell, and therefore not visible upon the internal moulds. The development of the bend shows rather conspicuous individual variation, probably due to differences in the pressure of the free edge of the preceding instar. In many specimens one (cf. Pl. XV, Fig. 7; HADDING 1913, Pl. VI, Figs. 14, 15) or two (cf. HADDING 1913, Pl. VI, Fig. 16) valves of earlier instars are retained, on other specimens the free edge of the preceding moult has left a more or less distinct furrow-like impression upon a part of the valve. The bend may be limited internally by the furrow, and the valve is then conspicuously thickened along the bend. In other cases the furrow is only indicated, and the inner boundary of the bend is then fairly indistinct (cf. Pl. XV, Fig. 9; HADDING 1913, Pl. VI, Fig. 10). The surface of the valve outside the bend slopes rather steeply, more in specimens with a distinct bend, less in those with only an indication of it. The dorsal area of the valve slopes steeply towards the dorsum.

Posterior cardinal corner field flattened, usually limited by an indistinct furrow or a distinct change in convexity. Anterior cardinal corner field convex, poorly delimited from the remainder of the valve. The groove inside the left valve along the free margin is apparently not developed. Closure of the carapace not accessible for observation.

Surface of the valve apparently smooth, without any trace of ornamentation.

DIMENSIONS.—See Table 37. All measured specimens have been found in the exposure No. III: 6 of Röstånga, Scania. *Nemagraptus gracilis* zone.

DISCUSSION.—There does not seem to exist any doubt that the specimens with one or two adherent valves (= *Primitia conchoides* in HADDING 1913) and those without any retained valve of the preceding moult stages (= *P. tolli* in HADDING op. cit.) belong to a single species. All these different types occur occasionally on the same slab of the shale. In some specimens examined a part of the still adhering valve of the preceding instar is broken off showing beneath it the continuation of the surface of the valve of the subsequent moult stage. It is also obvious that the rather considerable variability in the development of the concentric furrows and of the bend is due to the differences in the pressure of the free edge of the preceding instar.

Conchoprimitia? conchoides differs rather considerably from the other species of the genus, and later studies may prove the neccessity of removing it into a separate genus. The main differences from the other species of *Conchoprimitia* are the distinctness of the adductor scar upon the lateral surface, the

Table 37.

No.	Mus. cat. no.	L. valve	H. valve	H-L	Valve	Remarks
1	LM 2509 t	1.47	0.95	—	r	Pl. XV, Fig. 8; HADDING 1913, Pl. VI, Fig. 11.
2a	LM 2513 t	1.25	~0.88	—	l	Lectotype. Pl. XV, Fig. 7; HADDING 1913, Pl. VI, Fig. 15.
2b	,,	1.01	0.62	—	l	Retained valve of preceding instar upon the specimen No. 2a.
3	LM 2508 t	1.15	0.69	0.76	r	HADDING 1913, Pl. VI, Fig. 10.
4	LM	1.13	0.68	—	r	Figured on Pl. XV, Figs. 9–11.
5	LM	1.09	0.71	—	r	
6a	LM 2512 t	0.93	~0.62	—	r	HADDING 1913, Pl. VI, Fig. 14.
6b	,,	0.71	0.46	—	r	Retained valve of preceding instar upon the specimen No. 6a.
7	LM 2511 t	0.90	0.58	—	r	HADDING 1913, Pl. VI, Fig. 13.

presence of an adventral bend, and the steeply sloping peripheral area of the valve.

OCCURRENCE.—The vertical distribution of *C.? conchoidea* in the *Dicellograptus* shale of the Fågelsång district, Scania, is illustrated by HEDE (1951, Table 4; "*Primitia*" *tolli* + *Conchoprimitia conchoides*). The species has been recorded (as "*Primitia*" *tolli* HADDING) also from the superimposed Sularp shale of the district (LINDSTRÖM 1953). Specimens belonging probably to *C.? conchoidea* occur in the lower and middle parts of the *Ludibundus* mudstone in Västergötland (Norra Skagen and Kullatorp borings, Kinnekulle). Some small specimens from the latter district agree closely with the Scanian material, the lateral surface of the valve of large specimens is, however, always somewhat corroded, and does not show the characteristic elevated and rounded mark of the adductor scar. The specimens from Kinnekulle also attain a considerably larger size than those from Scania. Until better preserved material is available the specific identity of the former specimens remains somewhat uncertain.

Gen. *Parapyxion* n. gen.

TYPE SPECIES.—*Primitia subovata* THORSLUND, 1948.

DERIVATION OF THE NAME.—From Greek παρά = near + *Pyxion*, alluding to the similarity to the genus *Pyxion*.

DIAGNOSIS.—Non-sulcate to unisulcate, sulcal structure, if developed, faint to fairly deep. Dorsal area of the valve steeply sloping, but not protruding beyond the hinge-line; peripheral area of the valve along the free margin gently sloping, without marginal depression, and in some species with only a faint, bend-like adventral thickening of the shell. Mark of the adductor scar upon

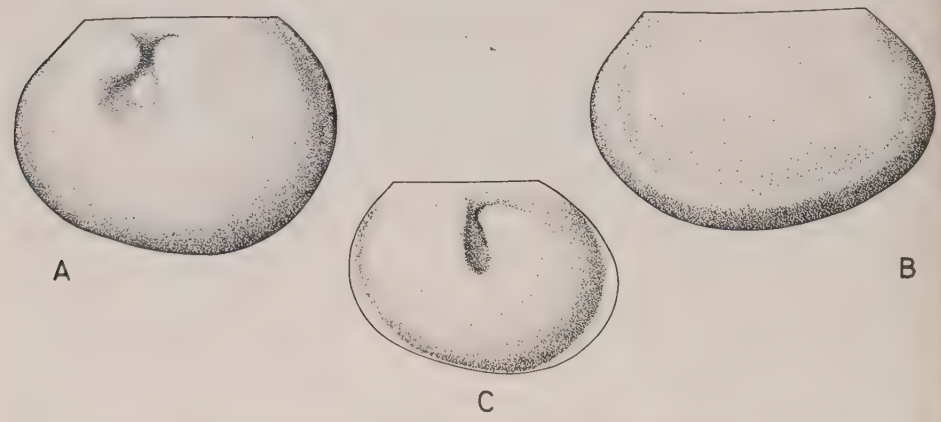


Fig. 46. Reconstruction of some leperditellids. A, *Parapyxion subovatum* (THORSL.); B, *Pyxion carinatum* (HADDING); C, *Craspedopyxion undulosum* (ÖPIK). ×35.

the lateral surface well-defined, rounded, moderately large, situated in the centre of a faint depression close to the dorsal bend of the valve and well in front of the mid-length of the valve. Surface of the valve antero- and posterodorsally of the scar faintly to moderately inflated. Outline rounded, distinctly postplete. Closure of the carapace unknown.

SPECIES.—*Primitia prunella* BARRANDE, 1872
Primitia subovata THORSLUND, 1948
Primitia obesa THORSLUND, 1948.

GENERIC CHARACTERS.—Outline in all species distinctly postplete with a comparatively high (tr.) postadductorial area. The part of the surface of the valve which corresponds to the dorsum in e.g. *Conchoprimitia*, narrow, orthocline to slightly epicline, more or less plane merging in ventral direction smoothly into the surface of the dorsal area of the valve. It is difficult to draw a distinct boundary between the real dorsum and the adjacent part of the surface of the valve, and for this reason the term dorsum is extended in this case as well as in related genera (*Pyxion*, *Craspedopyxion*) to comprise the whole steeply sloping dorsal area of the valve. With this delimination the dorsum of *Parapyxion* is high, steeply sloping, almost orthocline to somewhat hypocline, but never distinctly epicline. Its ventral boundary is formed by a broadly rounded bend.

Mark of the adductor scar upon the lateral surface generally distinct, moderately large, circular, situated close to the dorsal bend of the valve and well in front of the mid-length of the valve. It usually lies in the centre of a circular depression which is well-defined in *P. subovatum*, but faint and poorly delimited in *P. obesum* and *P. prunellum*. In the type species this depression is dorsally continuous with a fairly deep, narrow sulcus which extends in dorsal direction up to the ventral part of the dorsum. In the two other species the sulcal structure

is missing or forms only a faint, scarcely distinguishable depression. In *P. subovata* the surface of the valve is conspicuously swollen in front of as well as behind the ventral part of the sulcus, in the other species these inflations are flattened and scarcely distinguishable. In the former species both inflations are connected by a low, rounded elevation which surrounds the depression with the scar.

The peripheral area of the valve along the free margin is fairly uniformly convex, sloping more or less gently towards the free margin. In some specimens of *P. subovata* the adventral area of the valve is slightly thickened, forming an indication of a carinal bend.

Discussion.—The development of the sulcal and lobal structures varies rather considerably between the species included here in *Parapyxion*. The general features of the valve, as the high, ortho- to hypocline dorsum, the position of the always distinct, circular adductor scar, the general pattern of the sulcation and lobation, and the general shape and convexity of the valve, are common to all these species. Thus in this case as well as in *Conchoprimitia* and several other leperditellid genera the distinctness and prominence of the sulcal and lobal structures alone do not seem to be of generic importance.

The general appearance of *P. subovatum* recalls that of the type species of *Pseudulrichia*, *P. bivertex* Ulrich, 1897. The latter species is still poorly known. The latest published figure of *P. bivertex* (Bassler 1919, Pl. 55, Fig. 32) shows a slightly preplete outline and two prominent, rounded nodes close to the dorsal margin of the valve. The reason of including this species in *Dicranella* (Bassler & Kellett 1934, p. 286) is not clear. If the published figures of the type species of *Pseudulrichia* are correct, this genus differs distinctly from *Parapyxion*. *Milleratia* shows a depressed marginal area and a strongly epicline dorsum (Swartz 1936, Pl. 86, Fig. 7). *Pyxion* differs by a larger adductor scar, well-defined carinal ridge, longer and narrower valves, and other features, and *Eridoconcha* by the strongly epicline dorsum, absence of a distinct adductor scar upon the lateral surface, and by the conspicuous adventral thickening of the shell.

Occurrence.—Middle and Upper Ordovician of Sweden and Bohemia. The type species appears in the middle part of the *Ludibundus* beds and is the earliest known species of the genus.

Parapyxion subovatum (Thorslund, 1948)

Pl. XV, Figs. 16–19; Text-fig. 46A.

1948 *Primitia subovata* n.sp.—Thorslund, p. 365, Pl. XX, Fig. 5.

Holotype.—Left valve, UM no. Vg. 17, figured on Pl. XV, Figs. 18–19, Thorslund 1948, Pl. XX, Fig. 5.

Type Locality.—Västergötland, Kinnekulle, Kullatorp boring.

TYPE STRATUM.—*Ludibundus* mudstone, at the level of 77.42 m of the core.

DIAGNOSIS.—Sulcus fairly deep, extending up to the ventral part of the dorsum. Elevations in front of and behind the ventral part of the sulcus prominent, continuing ventrally in low, rounded elevations on either side of the adductorial depression. Ornamentation consisting of densely spaced, low, poorly defined granules.

MATERIAL.—Numerous valves.

DESCRIPTION.—Outline distinctly postplete, ovate. Dorsum high, dorsal part plane, more or less orthocline, ventral part convex, hypocline, higher than the dorsal part. Highest convexity slightly in front of the mid-length of the valve, close to the dorsal margin of the lateral surface of the domicilium. Adductor scar distinct, circular, smooth, lying in the centre of a faint, circular depression which continues in dorsal direction into a comparatively narrow (tr.), short, and deep sulcus. Surface of the valve in front of and behind the ventral part of the sulcus inflated, forming two knob-like, low prominences which continue ventrally into a rounded, poorly defined elevation on either side of the adductorial depression. The specimens examined show a rather considerable variability in the shape and distinctness of the lobal structures. In large specimens the elevations are as a rule lower and less distinct than in small valves; the elevations in front of and behind the adductorial depression are usually united ventrally of the latter so that the adductorial depression and the ventral part of the sulcus are surrounded by a continuous horseshoe-shaped rounded ridge with expanded and protruding dorsal ends. In smaller specimens the elevations on either side of the adductorial depression are as a rule more prominent and not confluent ventrally. The top of the elevation behind the ventral part of the sulcus lies invariably higher than that in front of the sulcus, and forms the highest point of the valve.

The surface of the valve slopes fairly gently towards the free margin except anterodorsally, where it slopes almost vertically. In some specimens a faint concentric furrow can be observed close to the free edge (impression of the free edge of the valve of the preceding instar?). In some moderately large specimens the elevation in front of the sulcus continues ventrally in a conspicuous bend-like adventral thickening resembling the carinal ridge in *Pyxion*.

Owing to the rather considerable variation of the lobal and adventral features the material of *P. subovata* seemed at first sight to contain several closely related species. A closer study of the abundant material revealed, however, a complete transition from one extreme type to the others, and the differences seem, therefore, to be due to individual variation.

The ornamentation consists of closely spaced, low and poorly defined granules which are scarcer or almost absent close to the free margin. The surface of the valve is, however, poorly preserved in all specimens examined, and the details of the ornamentation could not be clearly observed.

DIMENSIONS.—See Table 38.

Table 38.

No.	Mus. cat. no.	L. valve	H. valve	H-L	Valve	Locality	Remarks
1	UM Vg. 17	1.33	0.93	0.83	l	Kullatorp 77.42 m	Holotype. Pl. XV, Figs. 18–19; Thorslund 1948, Pl. XX, Fig. 5.
2	UM Vg. 713	1.19	0.83	0.69	l	,, 76.84 m	Figured on Pl. XV, Figs. 16–17.
3	SGU	1.27	0.86	0.77	l	Norra Skagen 5.92 m	
4	,,	1.20	0.77	0.72	l	,, ,, 3.80 m	
5	,,	1.19	0.82	0.70	r	,, ,, 5.23 m	
6	,,	1.07	0.72	—	l	,, ,, 4.02 m	

Discussion.—Numerous well-preserved topotype specimens of *P. prunella* (Barr.) (RM) have been examined. The figures published by Barrande (1872, Pl. 26, Figs. 5–6) hardly give a correct impression of the real characters of the species, and a future re-description is necessary. *Parapyxion prunella* resembles *P. subovata*, but differs by its attaining a much larger size, almost obsolete sulcal and lobal structures, and by the ornamentation which consists of coarse, closely set pits.

Occurrence.—Middle and upper parts of the *Ludibundus* beds. Västergötland: Norra Skagen and Kullatorp bores.

Gen. *Pyxion* Thorslund, 1948

Type Species.—*Primitia carinata* Hadding, 1913.

Diagnosis.—Nonsulcate to unisulcate, with or without a faint, broad sulcal depression dorsally and anteroventrally of the adductor scar. Mark of the adductor scar, if distinguishable on the lateral surface, fairly large, circular, situated close to the dorsal bend and well in front of the mid-length of the valve. In front of the adductor scar a rather large, oblong knob, and behind the scar occasionally a large, low inflation. Valves elongate, postplete, hingeline fairly long, dorsum high, convex, ortho- to hypocline. Lateral surface of the valve along the free margin surrounded by a rounded carinal ridge which reaches the dorsal margin of the valve at the cardinal corners. Peripheral area of the valve steeply sloping in all directions. No marginal depression. Closure of the carapace unknown.

Species.—*Primitia carinata* Hadding, 1913

Pyxion kinnekullensis Thorslund, 1948.

Discussion.—*Pyxion* resembles *Parenthatia* and certain species of *Eridoconcha* as e.g. *E. elegantula* Keenan (1951, Pl. 79, Figs. 17–18). *Parenthatia* has a much higher carinal ridge, a depressed marginal area (cf. Kay 1940, Pl. 32,

Fig. 44), and does not show the *Pyxion*-type of lobation. *Eridoconcha* differs by the strongly epicline dorsum, a deeper and better defined sulcus, and the presence of a node behind the sulcus.

Occurrence.—See the type species, p. 429. *Pyxion kinnekullensis* has been found in the Kullatorp core in the same beds as *P. carinatum* (cf. Thorslund 1948, p. 348).

Pyxion carinatum (Hadding, 1913)

Pl. XV, Figs. 12–15; Text-fig. 46B.

1913 *Primitia carinata* n.sp.—Hadding, p. 68, Pl. VI, Fig. 12.
1948 *Pyxion carinatus* (Hadding)—Thorslund, p. 367, Pl. XX, Figs. 1–2.

Lectotype (designated by Thorslund 1948, p. 373).—Right valve, LM no. 2510 T, Hadding 1913, Pl. VI, Fig. 12, Thorslund 1948, Pl. XX, Fig. 2, in the present paper Pl. XV, Figs. 12–15 (see also Text-fig. 46B).

Type Locality.—Scania, Röstånga, locality No. III: 13.

Type Stratum.—*Nemagraptus gracilis* shale.

Diagnosis.—No distinct sulcal depression dorsally of the adductor scar; carinal ridge low, rounded, bend-like. Lateral surface of the valve flattened, low, in ventral view hardly protruding beyond the carinal ridge. No apparent ornamentation.

Description.—Outline slightly postplete. Dorsum, as defined above, p. 424, high, dorsal part narrow, plane, more or less orthocline, ventral part high, convex, hypocline, merging posteriorly smoothly into the posterior, gently sloping area of the valve. Lateral surface of the valve flattened, slightly convex. Mark of the adductor scar circular, fairly large, distinct in the lectotype, poorly defined or not recognizable in the other specimens examined. It is situated close to the dorsal bend, and well in front of the mid-length of the valve. Surface of the valve in front of the scar conspicuously inflated, forming an anterodorsally oblong knob, its top forming the highest point of the valve. Behind the scar a broad, low inflation extending posteriorly almost to the carinal ridge. Dorsally of the scar the surface is somewhat depressed, the depression being, however, too faint and too poorly defined to be called a sulcal structure. Lateral surface of the valve surrounded along the free margin by a low carinal ridge which is rounded ventrally. Thorslund's figures of this species do not give a quite correct impression of the carinal structure, the ridge seeming to possess too sharp an edge. The summit of the ridge lies only slightly lower than the top of the posterodorsal inflation. In anterodorsal and posterodorsal direction the carinal ridge curves towards the free margin reaching the dorsal margin of the valve at the cardinal corners (cf. Pl. XV, Fig. 12). The proximal areas of the valve are high, and slope steeply in all directions. No ornamentation has been observed.

Dimensions.—See Table 39.

Table 39.

No.	Mus. cat. no.	L. valve	H. valve	H-L	Valve	Locality	Remarks
1	LM 2510 T	1.32	0.86	0.85	r	Röstånga III: 13	Lectotype.
2	UM Vg. 14	1.42	0.87	—	l	Kullatorp 76.80 m	Thorslund 1948, Pl. XX, Fig. 1.
3	UM Vg. 714	1.39	0.81	—	r	Kullatorp 78.19 m	

Discussion.—*Pyxion kinnekullensis* Thorsl. differs from *P. carinatum* by a conspicuous sulcal depression dorsally of the adductor scar, a more prominent, rounded carinal ridge, and a more convex lateral surface of the valve which protrudes considerably beyond the carinal ridge in ventral view.

Occurrence.—Scania, Röstånga (*Nemagraptus gracilis* shale) (cf. Hadding 1913). Västergötland, Kinnekulle, Kullatorp boring (middle part of the *Ludibundus* beds) (4 valves).

Gen. *Craspedopyxion* n. gen.

Pl. XIV, Figs. 9–11; Text-fig. 46C.

Type Species.—*Primitia undulosa* Öpik, 1937.

Derivation of the Name.—From Greek κράσ–πεδον, border + *Pyxion*, referring to the distinct marginal border-like depression and the probable relationship to the genus *Pyxion*.

Diagnosis.—Unisulcate, no distinct mark of the adductor scar upon the lateral surface; sulcus short (tr.), deep, extending up to the ventral part of the dorsum, situated almost at the mid-length of the valve. Surface of the post-adductorial area inflated behind the sulcus, forming a prominent node; no other lobal structures. Outline postplete, roughly semicircular; valves small, strongly convex, with a distinct flattened marginal border which is broader anteriorly and posteriorly than ventrally. Dorsum comparatively high, hypocline. Closure of the carapace unknown.

Discussion.—Only the type species is known (cf. Öpik 1937, Pl. I, Fig. 1a–b, Pl. VI, Fig. 1a–b; in the present paper Pl. XIV, Figs. 9–11, Text-fig. 46C). Three topotype specimens (UM) were examined. *Craspedopyxion undulosum* differs from the other leperditellacean genera by its strongly convex valves, nearly semicircular outline, the position of the sulcus, presence and shape of the flattened margin along the free edge, and by the strongly hypocline dorsum. *Milleratia* has, in some species at least, a similar depressed margin, but differs from *Craspedopyxion* by the prominent, epicline dorsum, the anterior position of the sulcus, and the outline of the valve. *Parapyxion* resembles in the shape of the dorsum and of the sulcus, but differs by the

absence of a depressed margin, anterior position of the sulcus, the outline of the valve, and by the presence of a distinct mark of the adductor scar upon the lateral surface.

Occurrence.—Estonia: Kohtla zone of the Kukruse Stage ($C_{II}\alpha$; cf. Sarv 1956a, p. 51).

Stratigraphical Distribution of the Ostracode Species

Stratigraphical Remarks.—The sequence of the *Ludibundus* limestone treated below extends up to the bentonite beds. The latter beds and the beds between them and the *Macrourus* limestone (or the *Dicranograptus clingani* shale) are not included. Within the *Ludibundus* limestone a lower part, comprising the lowermost 2–3 m in Västergötland and 5–6 m in the other districts, is provisionally distinguished (L in the Table 40). The beds between the lower part and the bentonite beds are referred to as the middle part of the *Ludibundus* limestone (M in the Table). Erratic boulders of the Tvären area are considered as belonging exclusively to the lower part of the *Ludibundus* beds.

The South Bothnian erratic boulder Bergsbrunna No. 1 which was previously (Jaanusson 1953, pp. 416–417) regarded as contemporaneous with $C_{II}\alpha$ in Estonia is here provisionally considered as representing the topmost *Crassicauda* limestone. The recent information about the vertical distribution of the species in the boundary region between $C_I c$ and C_{II} seems to indicate a late Uhakuan ($C_I c$) age for this boulder.

Discussion.—The vertical distribution of the described species will be treated in a future series of papers on the *Platyurus* Stage and the Middle Ordovician of southern and central Sweden (excl. Scania). Here only some general trends of the distribution are exposed.

The boundary between the *Gigas* and *Platyurus* limestones is well expressed by the ostracode fauna. The former division is characterized by the common occurrence of *Conchoprimitia* cf. *circumstriata* (Hessland) and by the presence of the genera *Aulacopsis*, *Glossomorphites*, and *Pinnatulites*. The last three genera are unknown in strata younger than the *Gigas* limestone.

The commonest species in the *Platyurus* limestone are *Euprimites effusus* and *Laccochilina* (*Laccochilina*) *bulbata*. In this division the genera *Chilobolbina*, *Piretia*, and *Piretella* make their appearance. Also *Sigmobolbina*- and *Levisulculus*-like forms have been encountered, but the available material is too poorly preserved for description or a safe generic reference. *Piretia geniculata* is a wide-spread species and characteristic for this division.

Euprimites effusus is the commonest species also in the *Schroeteri* limestone of all districts except Västergötland, where this species has not been found. In the latter district *Actinochilina* sp. A is of common occurrence. *Steusloffia linnarssoni* and several species of *Tallinnella* make their appearance.

Common species in the *Crassicauda* limestone are: *Laccochilina* (*Laccochilina*) *paucigranosa*, *Euprimites bursellus*, *Tallinnella dimorpha*, *Steusloffia linnarssoni*, and *Sigmobolbina sigmoidea*. *Sigmoopsis* and *Platybolbina* are hitherto unknown from beds older than the *Crassicauda* limestone.

The lower part of the *Ludibundus* limestone has yielded a particularly great number of described species of *Palaeocopa*. This is due mainly to the abundance and good state of preservation of the ostracodes in the boulders of the Tvären area. Of the 34 species hitherto recognized from these beds in central and southern Sweden 19 have been found exclusively in the boulders of the Tvären area, and 5 additional species (*Platybolbina kapteyni*, *Tvaerenella carinata*, *Euprimites suecicus*, *Hesperidella esthonica*, and *Balticella oblonga*) only in these boulders and in the Lockne area of Jämtland, northern Sweden. In the latter area certain beds of the lower *Ludibundus* limestone abound with well-preserved ostracodes though the state of preservation is not quite equal to that of the Tvären area. In the Lockne area two further species have been described (Thorslund 1940) which have not been found outside this area (*Lomatobolbina mammillata* and *Carinobolbina? jemtlandica*), and the collections include several other, undescribed species not known from other districts.

The commonest species in the *Ludibundus* limestone are *Euprimites locknensis* and *Steusloffia costata*. These two species range through the whole extension of this division, and occur abundantly also in the mudstones of Västergötland. Curiously enough, none of these species has been found in the boulders of the Tvären area.

The lower part of the *Ludibundus* beds is characterized by the occasionally common occurrence of *Steusloffia multimarginata*, *Conchoprimitia leperditioidea*, *Tallinnella dimorpha*, and *Uhakiella* cf. *coelodesma*. The two last species occur abundantly in the Uhaku (*Crassicauda*) beds, and their presence in the lower *Ludibundus* limestone gives the fauna of these beds an appearance of a mixed fauna consisting of species which have survived from the *Crassicauda* limestone as well as of new immigrants.

The ostracode fauna of the *Ludibundus* mudstone of Västergötland as well as of the corresponding beds of Scania differs considerably from that of the other districts. This fauna is characterized by *Conchoprimitia? conchoidea*, *Actinochilina suecica*, *Parapyxion subovatum*, *Pyxion*, and *Primitiella? spiniger*, all of them hitherto unknown outside Västergötland and Scania. The above difference in the ostracode fauna is apparently of ecological nature. A comparable difference exists also between the *Schroeteri* mudstone of Västergötland and the contemporaneous limestone of the other districts.

The above Table does not give a perfectly correct idea of the real distribution of the palaeocope genera. In order to safely determine small species of palaeocopes well-preserved material is needed, and for description of a new species as well as for safe generic reference both dimorphs ought to be known in the case of dimorphic genera. If certain parts of the sequence studied had con-

Table 40. Vertical distribution of the ostracode species in central and southern Sweden.

Abbreviations:

B, found exclusively in the South Bothnian erratic boulder Bergsbrunna No. 1.
L, lower part of the *Ludibundus* beds.
M, middle part of the *Ludibundus* beds.
T, found exclusively in the erratic boulders of the Tväre area, Södermanland.
V, found only in Västergötland and/or Scania.
l, found in the lower part of the stage.
u, found in the upper part of the stage.

	Platy-urus	Schroe-teri	Crassi-cauda	Ludibundus L	Ludibundus M
Chilobolbina aff. *dentifera* (Bonnema)	—	—	+	—	—
sudermannica n. sp.	—	—	—	T	—
lativelata n. sp.	+	+	—	—	—
Laccochilina (*Laccochilina*) *paucigranosa* n. sp.	—	—	+	—	—
sp. A	—	—	+	—	—
sp. B	—	—	B	—	—
sp. C	—	—	—	T	—
bulbata n. sp.	+	l	—	—	—
Laccochilina (*Prochilina*) *decumana* (Bonnema)	—	—	—	+	—
ostrogothica n. sp.	—	u	+	—	—
Actinochilina suecica (Thorslund)	—	—	—	—	V
sp. A	—	V	—	—	—
Platybolbina kapteyni (Bonnema)	—	—	—	+	—
ampla n. sp.	—	—	—	T	—
inflata n. sp.	—	—	—	T	—
Oepikella tvaerensis Thorslund	—	—	—	T	—
bonnemai (Öpik)	—	—	—	T	—
Piretella tridactyla n. sp.	+	—	—	—	—
Piretia geniculata n. sp.	+	—	—	—	—
clypeolaria n. sp.	+	—	—	—	—
Uhakiella cf. *coelodesma* Öpik	—	—	—	+	—
aequigranosa n. sp.	—	—	+	—	—
periacantha n. sp.	—	—	B	—	—
Tvaerenella carinata (Thorslund)	—	—	—	+	—
Euprimites effusus n. sp.	+	+	—	—	—
anisus n. sp.	+	—	—	—	—
lockensis (Thorslund)	—	—	—	+	+
bursellus n. sp.	—	+	+	—	—
cf. *eutropis* (Öpik)	—	—	+	—	—
minor (Thorslund)	—	—	—	T	—
suecicus (Thorslund)	—	—	—	+	—
Levisulculus lineatus n. sp.	—	—	—	T	—
troedssoni (Thorslund)	—	—	—	T	—
granulosus (Thorslund)	—	—	—	T	—
? *reticulatus* (Thorslund)	—	—	—	T	—
Hesperidella esthonica (Bonnema)	—	—	—	—	—
Bolbina sp. A	—	—	—	T	—

Table 40 (*continued*)

	Platy-urus	Schroe-teri	Crassi-cauda	Ludibundus L	Ludibundus M
Bolbina? sp. B	—	—	+	—	—
Lennukella europaea (Öpik)	—	—	B	—	—
Tallinnella dimorpha Öpik	—	—	+	+	—
cf. *angustata* (Krause)	—	u	—	—	—
pachydactyla n.sp.	—	l	—	—	—
sebyensis n.sp.	—	+	—	—	—
cf. *lata* (Krause)	—	u	—	—	—
Steusloffia linnarssoni (Krause)	—	+	+	—	—
multimarginata Öpik	—	—	—	+	—
costata (Linnarsson)	—	—	—	+	+
Sigmoopsis platyceras (Öpik)	—	—	—	—	+
bergsbrunnae n.sp.	—	—	+	—	—
sp. A	—	—	—	T	—
sp. B	—	—	V	—	—
Polyceratella kuckersiana (Bonnema)	—	—	—	+	—
bonnemai Thorslund	—	—	—	T	—
Sigmobolbina sigmoidea n.sp.	—	?	+	—	—
pentagona n.sp.	—	—	—	T	—
variolaris (Bonnema)	—	—	—	T	—
Lomatobolbina craspedota n.sp.	—	—	—	T	—
Oezematobolbina nitens n.sp.	—	—	—	T	—
sp. A	—	—	—	T	—
Oepikium sp. A	—	—	+	—	—
Conchoprimitia leperditioidea Thorslund	—	—	—	+	—
? *conchoidea* (Hadding)	—	—	—	V	V
Parapyxion subovatum (Thorslund)	—	—	—	—	V
Pyxion carinatum (Hadding)	—	—	—	—	V
kinnekullensis Thorslund	—	—	—	—	V
Balticella oblonga Thorslund	—	—	—	+	—
"*Macronotella*" *kuckersiana* (Bonnema)	—	—	—	+	—
Primitiella? *spiniger* M. Lindström	—	—	—	—	V
"*Ulrichia*" *reticulata* Thorslund	—	—	—	—	V

tained ostracodes in a state of preservation similar to that of the boulders of the Tvären area the number of described species and genera would have been considerably larger in these divisions. This applies particularly to finely nodular limestones and marls of the *Platyurus* and *Schroeteri* beds of Östergötland which abound with poorly preserved and in part undeterminable ostracodes.

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Postscript

When this paper had gone to press two important papers on palaeocope ostracodes printed in *Jour. Paleont.*, vol. 30, no. 5, reached Uppsala. In this publication Swartz & Whitmore (1956)[1] described dimorphism in the new primitiopsid genus *Limbinaria*. Of special interrest is their statement of Swartz having discovered the frill in the beyrichiid genera *Velibeyrichia, Dibolbina*, and *Apatobolbina* and in the eurychilinid genus *Eurychilina* "to be a double walled structure, having internal partitions at the locations of the radial striae of the external surface". In Swartz' opinion, "the nature of this frill provides an important link between *Eurychilina* and *Velibeyrichia* that tends to support the arrangement of the eurychilinids and velibeyrichids in a single family, in the fashion that was proposed by Swartz in 1936". However, as pointed out above (p. 223), the development of the beyrichiids from eurychilinids involved the loss of the external, velar dimorphism and the formation of an internal, cruminal dimorphism, and until the course of these important changes is properly understood the degree

[1] Swartz, F. M. & Whitmore, F. C., Jr., 1956: Ostracoda of the Silurian Decker and Manlius limestones in New Yersey and Eastern New York. *Jour. Paleont.*, vol. 30, no. 5, pp. 1029–1091.

of relationship of *Beyrichiidae* and *Eurychilinidae* must be considered as unknown. An identical construction of the frill occurs also in the hollinacean genus *Oepikium*, and the possibility of the internally partitioned type of the frill having developed indepentently in eurychilinids and beyrichiids cannot be excluded.

In another paper in the above publication STOVER (1956)[1] described dimorphism in the hollinine genus *Hanaites* POKORNÝ, 1950, and established a new genus *Adelphobolbina* for the Devonian species referred by KESLING & TABOR (1952, 1953) to *Ctenobolbina*. The probability of these species belonging to a new genus was pointed out above (cf. pp. 409–410).

[1] STOVER, L. E., 1956: Ostracoda from the Windom shale (Hamilton) of western New York. *Jour. Paleont.*, vol. 30, no. 5, pp. 1092–1142. Menasha, Wis.

Plates

Unless otherwise stated, the specimens were whitened with ammonium chloride. Photographs by Mr. N. HJORTH, some of the figures slightly retouched by Mr. E. STÅHL.

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Plate I

All figures magnified ×25.

Chilobolbina sudermannica n. sp.

All specimens figured have been found in erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone.

1–2. Right tecnomorphic valve in lateral and dorsal view. UM no. T 165.
3. Holotype. Left heteromorphic valve in lateral view. UM no. T 141. Coll. P. Thorslund 1928.
4. Right tecnomorphic valve in ventral view. The frill is broken off. Observe the striation of the contact area between the frill and the domicilium. UM no. T 142.
5. Right heteromorphic valve in ventral view. The frill and the dolon are broken off. Observe the pronounced curve of the contact area between the dolon and the domicilium. UM no. T 171.

Chilobolbina dentifera (Bonnema, 1909)

Kukruse, Estonia. Kukruse Stage (probably $C_{II}\alpha$).

6. Right heteromorphic valve in lateral view. The frill is broken off. UM no. E 11.
7. Right tecnomorphic valve in lateral view. The frill is broken off. UM no. E 12.

Chilobolbina lativelata n. sp.

8. Right tecnomorphic valve showing the outline of the frill. Motala boring, at the level of 116.20 m. *Platyurus* limestone. SGU.
9. Right heteromorphic valve in lateral view. The frill is broken off. Öland, exposure between the village Lerkaka and the beach. Gray *Schroeteri* limestone. RM no. Ar. 19683. Coll. J. G. Andersson 1892.
10–11. Holotype. Right heteromorphic valve in ventral and lateral view. The anterior part of the frill is broken off. Motala boring, 111.63 m. Lowermost *Schroeteri* limestone. SGU.

Laccochilina (Laccochilina) paucigranosa n. sp.

All specimens figured have been found in the *Crassicauda* limestone.

12. Left heteromorphic valve in lateral view. South Bothnian erratic boulder Erken No. 10. UM no. B 286.
13–14. Left heteromorphic valve in lateral and ventral view. Siljan district, Furudal, quarry at the rivulet Kalkbergsbäcken. UM no. D 540.
15. Right heteromorphic valve in lateral view. Smedsby Gård boring, 117.33 m. SGU.
16–17. Holotype. Right heteromorphic valve in lateral and ventral view. South Bothnian erratic boulder Erken No. 10. UM no. B 287.

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Plate II

Magnification of Figs. 1–14, ×25, that of Figs. 15–16, ×20.

Laccochilina (Laccochilina) sp. A

1. Left heteromorphic valve in lateral view. Stora Åsbotorp boring, at the level of 50.01 m. *Crassicauda* limestone. SGU.

Laccochilina (Laccochilina) sp. B

2–3. Right heteromorphic valve in lateral and ventral view. South Bothnian erratic boulder Bergsbrunna No. 1. Uppermost *Crassicauda* limestone. UM no. B 300.
4. Left tecnomorphic valve in lateral view. Locality and horizon as in Figs. 2–3. UM no. B 301.

Laccochilina (Laccochilina) sp. C

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone.

5. Right tecnomorphic valve in lateral view. The frill is partly broken off. UM no. T 261.
6. Right heteromorphic valve in lateral view. Figured by THORSLUND 1940, Pl. 3, Fig. 11. UM no. T 29. Coll. P. THORSLUND 1931.
7–8. Left heteromorphic valve in ventral and lateral view. UM no. T 260.

Laccochilina (Laccochilina) bulbata n. sp.

9. A small right tecnomorphic valve with ornamentation differing from other specimens. Motala boring, at the level of 119.17 m. Lowermost *Platyurus* limestone. SGU.
10. Left heteromorphic valve in ventral view. The top of the postadductorial area is broken off. Gammalsby boring, 11.20 m. *Platyurus* limestone. SGU.
11. Right heteromorphic valve in lateral view. The dorsal plica and the top of the preadductorial area are broken off. Motala boring, 112.06 m. Lowermost *Schroeteri* limestone. SGU.
12. Left tecnomorphic valve in lateral view. Motala boring, 116.24 m. *Platyurus* limestone. SGU.
13. Right tecnomorphic valve in lateral view. The frill is partly broken off. Motala boring, 112.05 m. Lowermost *Schroeteri* limestone. SGU.
14. Holotype. Left heteromorphic valve in lateral view. The dorsal plica is partly broken off. Motala boring, 114.10 m. *Platyurus* limestone. SGU.

Laccochilina (Prochilina) decumana (BONNEMA, 1909)

15–16. Left heteromorphic valve in lateral and ventral view, the posterior spines partly broken off. Erratic boulder of the Tvären area. Lowermost *Ludibundus* limestone. UM no. T 250.

Plate III

Laccochilina (Prochilina) decumana (Bonnema, 1909)

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone. Magnification ×20.

1. Right tecnomorphic valve in lateral view. Posterior spines broken off. UM no. T 238. Coll. P. Thorslund 1928.
2. Left tecnomorphic valve in lateral view. UM no. T 241.
3. Right tecnomorphic valve in lateral view. Posterior spines partly broken off. UM no. T 243.
4. Left tecnomorphic valve in ventral view. The frill is removed in order to expose the subvelar field. UM no. T 273.

Laccochilina (Prochilina) ostrogothica n. sp.

All figures magnified ×25.

5. Left tecnomorphic valve in lateral view. Posterior spines broken off. Motala boring, at the level of 101.76 m. *Crassicauda* limestone. SGU.
6. Right heteromorphic valve in lateral view. Posterior spines partly broken off. South Bothnian erratic boulder Erken No. 10. *Crassicauda* limestone. UM no. B 299.

7–8. Holotype. Right heteromorphic valve in ventral and lateral view. Posterior spines broken off. Motala boring, 105.57 m. *Crassicauda* limestone. SGU.

Actinochilina suecica (Thorslund, 1948)

9. Holotype. Right tecnomorphic valve in lateral view. Figured by Thorslund 1948, Pl. XX, Fig. 8. Kinnekulle, Kullatorp boring, 71.50 m. *Ludibundus* beds. UM no. Vg 20. ×25.

Actinochilina cf. *suecica* (Thorslund, 1948)

10. Left tecnomorphic valve, partly preserved as internal mould, showing the posterior outline of the frill. Anteriorly the frill is broken off. Photographed without ammonium sulfide coating. Scania, Fågelsång district, boulders NNE of the Sularps Gård, on the south side of the new highway (loc. No. E 56). Coll. M. Lindström and C. F. Glimberg. LM. ×25. See also Pl. XIV, Fig. 8.

Actinochilina sp. A

11. Internal mould of a right tecnomorphic valve. Norra Skagen boring, 27.95 m. *Schroeteri* mudstone. SGU. ×25.
12. Right tecnomorphic valve. Norra Skagen boring, 28.55 m. *Schroeteri* mudstone. SGU. ×25.

Platybolbina ampla n. sp.

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone.

13–14. Holotype. Right heteromorphic valve in lateral and ventral view. UM no. T 227. ×25.
15. Small left tecnomorphic valve in lateral view. UM no. T 229. Coll. P. Thorslund 1928. ×50.
16. Right heteromorphic valve in lateral view. UM no. T 228. ×25.

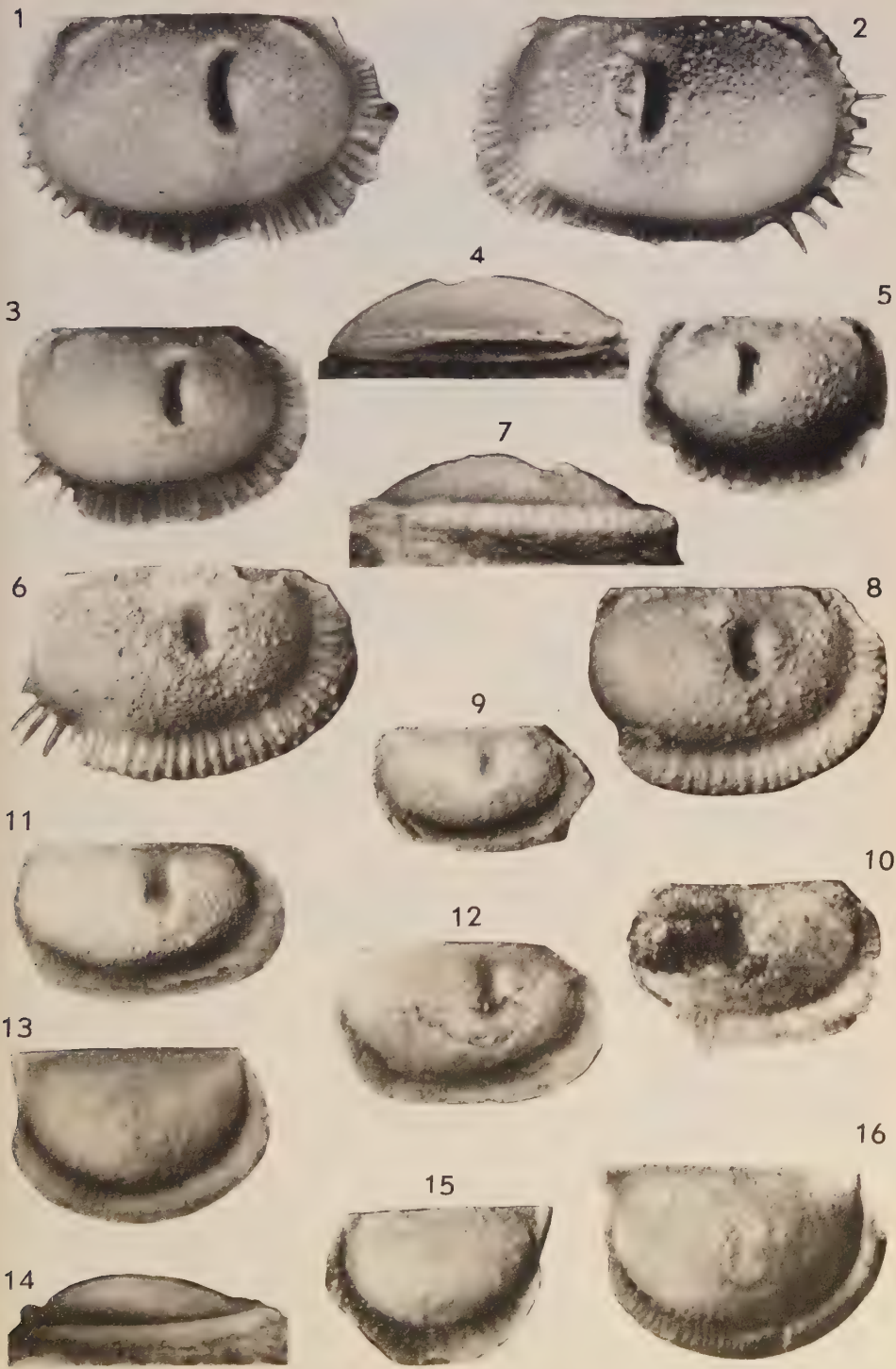
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Plate IV

Platybolbina kapteyni (Bonnema, 1909)

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone. Magnification × 37.5.

1. Right heteromorphic valve in lateral view. UM no. T 176.
2. Left heteromorphic valve in lateral view. UM no. T 177.
3. Right tecnomorphic valve in lateral view. UM no. T 189.

Platybolbina inflata n. sp.

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone.

4–5. Holotype. Right heteromorphic valve in ventral and lateral view. UM no. T 221. × 25.
6. Right tecnomorphic valve in lateral view. UM no. T 223. × 37.5.

Oepikella bonnemai (Öpik, 1937)

7–8. Left tecnomorphic valve in lateral and ventral view. Estonia, Kukruse. $C_{II}\alpha$. UM no. E 13. × 15.

Oepikella tvaerensis (Thorslund, 1940)

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone. Magnification × 15.

9–12. A small heteromorphic valve in lateral, posterior, dorsal, and ventral view. UM no. T 193. Coll. P. Thorslund 1928.
13. A small heteromorphic valve in posterior view. Figured by Thorslund 1940, Pl. 1, Fig. 4. UM no. T 3. Coll. P. Thorslund 1931.
14–15. A small left tecnomorphic valve in ventral and lateral view. UM no. T 206.
16. Tecnomorphic carapace in ventral view showing the closure of the carapace. The specimen is illuminated from behind in order to give a distinct picture of the marginal structures. UM no. T 210.
17. Right tecnomorphic valve in ventral view. UM no. T 201.
18–19. Right tecnomorphic valve in ventral and lateral view. UM no. T 220.

Piretia clypeolaria n. sp.

20. Holotype. Right heteromorphic valve in lateral view. Öland, Skärlöv boring, at the level of 5.35 m. *Platyurus* limestone. SGU. × 25.

Piretia geniculata n. sp.

21. Right tecnomorphic valve in lateral view. Öland, Böda Hamn boring, 20.73 m. *Platyurus* limestone. UM no. Öl. 127. × 37.5.
22. Holotype. Left heteromorphic valve in lateral view. Östergötland, Motala boring, 113.96 m. *Platyurus* limestone. SGU. × 37.5.

Bromidella reticulata Harris, 1931

23. Left heteromorphic valve in lateral view. Fitz oil pool, Oklahoma. Bromide formation. UM. × 25.

Plate V

Piretella tridactyla n. sp.

The specimens figured have been found in the *Platyurus* limestone. Magnification ×25.

1. Left tecnomorphic valve in lateral view. Östergötland, Motala boring, at the level of 116.04 m. SGU.
2–4. Holotype. Left tecnomorphic valve in lateral, dorsal, and ventral view. Östergötland, Motala boring, 116.28 m. SGU.
5. Internal mould of a left heteromorphic valve showing the extension of the dolon. Östergötland, Motala boring, 116.35 m. SGU.

Uhakiella cf. *coelodesma* Öpik, 1937

All figures magnified ×25.

6. Left heteromorphic valve. Västergötland, Kinnekulle, Kullatorp boring, 86.47 m. Lowermost *Ludibundus* beds. UM no. Vg. 87. Coll. P. Thorslund.
7–8. Right valve of a tecnomorphic carapace in lateral view and the whole carapace in ventral view. Tvären area, Ringsö, erratic boulder. Lowermost *Ludibundus* beds. UM no. T 95.
9. Right tecnomorphic valve in lateral view. Östergötland, Smedsby Gård boring, 96.37 m. *Ludibundus* limestone. SGU.

Uhakiella aequigranosa n. sp.

10. Holotype. Left heteromorphic valve. Siljan district, Fjäcka, locality No. 4. Uppermost *Crassicauda* limestone. UM no. D 427. ×25.
11. Right tecnomorphic valve. Öland, Gammalsby boring, 5.60 m. *Crassicauda* limestone. SGU. ×25.

Uhakiella periacantha n. sp.

South Bothnian erratic boulder Bergsbrunna No. 1. Uppermost *Crassicauda* limestone. Magnification ×25.

12. Left tecnomorphic valve in lateral view. Part of the marginal spines broken off. UM no. B 226.
13–14. Holotype. Left heteromorphic valve in lateral and ventral view. Marginal spines broken off. UM no. B 211.
15. Left heteromorphic valve in lateral view. Marginal spines broken off. UM no. B 212.
16–17. Right heteromorphic valve in ventral and lateral view. Marginal spines broken off. UM no. B 213.

Bolbina sp. A

18–19. Left heteromorphic valve in lateral and ventral view. Tvären area, Ringsö, erratic boulder. Lowermost *Ludibundus* limestone. UM no. T 109. ×25.

Bolbina? sp. B

20. Left valve of a probably heteromorphic carapace in lateral view. South Bothnian erratic boulder Erken No. 10. *Crassicauda* limestone. UM no. B 235. ×37.5.

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Plate VI

Hesperidella esthonica (Bonnema, 1909)

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone. Magnification ×37.5.

1. Right heteromorphic valve in lateral view. UM no. T 134.
2–3. Right tecnomorphic valve in lateral and dorsal view. UM no. T 136.

Tvaerenella carinata (Thorslund, 1940)

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone.

4. Tecnomorphic carapace in ventral view. Velar structure poorly developed. UM no. T 81. ×37.5.
5. Right tecnomorphic valve in lateral view. UM no. T 79. Coll. P. Thorslund 1928. ×25.
6. Right valve of a heteromorphic carapace in lateral view. UM no. T 87. ×25.
7–8. Right tecnomorphic valve in lateral and ventral view. Velar structure developed as a conspicuous ridge. UM no. T 88. ×25.
9. Left tecnomorphic valve in lateral view. UM no. T 80. ×25.

Euprimites effusus n. sp.

All figures magnified ×25.

10. Right heteromorphic valve with a comparatively short dolon in lateral view. Öland, Seby. Gray *Schroeteri* limestone. UM no. Öl. 120.
11. Holotype. Left heteromorphic valve in lateral view. Östergötland, Motala boring, at the level of 108.20 m. *Schroeteri* limestone. SGU.
12–13. Tecnomorphic carapace in dorsal view and its left valve in lateral view. Öland, Gammalsby bore, 9.92 m. *Schroeteri* limestone. SGU.
14–15. Left tecnomorphic valve in lateral and ventral view. Siljan district, Vikarbyn. *Schroeteri* limestone, div. *a*. UM no. D 425. m = marginal ridge.
16. Right tecnomorphic valve in ventral view showing the distinct admarginal ridge (a). Öland, Seby. Gray *Schroeteri* limestone. UM no. Öl. 121.

Euprimites anisus n. sp.

The specimens figured have been found in the *Platyurus* limestone. Magnification ×25.

17. Holotype. Right heteromorphic valve in lateral view. Posterior cardinal corner broken off. Öland, Böda Hamn boring, 22.40 m. UM no. Öl. 118.
18. Right heteromorphic valve in lateral view. Reticulation on the lateral surface of the domicilium poorly visible. Öland, Böda Hamn boring, 22.65 m. UM no. Öl. 119.
19. A fragmentary tecnomorphic carapace in ventral view showing the marginal structures. Left valve with a marginal ridge (m), right valve with an admarginal ridge (a). The posterior part of the left valve is broken off, and the slightly protruding free edge of the right valve (f) exposed. Öland, Gammalsby boring, 11.19 m. SGU.

Plate VII

Euprimites locknensis (THORSLUND, 1940)

The specimens figured have been found in the *Ludibundus* limestone. Magnification ×25.

1. Right heteromorphic valve in lateral view. Jämtland, exposure 1.2 km W of Tandsbyn railway station. SGU. Coll. P. THORSLUND 1935.
2. Right heteromorphic valve in lateral view, Öland, exposure at the beach of Böda Hamn. RM no. Ar. 20125. Coll. J. G. ANDERSSON 1893.
3. Right heteromorphic valve in lateral view. The dolon is broken off. Öland, Böda Hamn boring, at the level of 1.70 m. UM no. Öl. 116.

4–5. Right tecnomorphic valve in lateral and ventral view. The admarginal ridge is distinct, the area between the latter and the free edge not quite clearly visible. Locality as in Fig. 1. SGU. Coll. P. THORSLUND 1935.

6–7. Left tecnomorphic valve in lateral and ventral view. Note the distinct marginal ridge. Locality as in Fig. 2. RM no. Ar. 20129. Coll. J. G. ANDERSSON 1893.

Euprimites cf. *eutropis* (ÖPIK, 1937)

Magnification ×25.

8. Right heteromorphic valve in lateral view. Östergötland, Smedsby Gård boring, 119.40 m. Uppermost *Crassicauda* limestone. SGU.
9. Right heteromorphic valve. South Bothnian erratic boulder Erken No. 10. *Crassicauda* limestone. UM no. B 234.
10. Right valve of a heteromorphic carapace. South Bothnian erratic boulder Bergsbrunna No. 1. Uppermost *Crassicauda* limestone. UM no. B 231.
11. Right tecnomorphic valve. Locality and horizon as in Fig. 10. UM no. B 233.

Euprimites minor (THORSLUND, 1940)

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone. Magnification ×37.5.

12–13. Left tecnomorphic valve in lateral and ventral view. UM no. T 98. Coll. P. THORSLUND 1928.

14. Left heteromorphic valve in lateral view. The peripheral part of the dolon is broken off. UM no. T 97. Coll. P. THORSLUND 1931.
15. Left heteromorphic valve in lateral view. The reticulation is very faint. UM no. T 96.

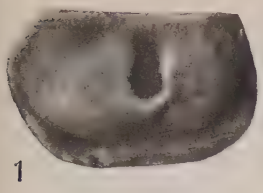
Euprimites bursellus n. sp.

16. Holotype. Left heteromorphic valve in lateral view. Öland, Böda Hamn boring, 12.02 m. Lowermost *Crassicauda* limestone. UM no. Öl. 113. ×25.
17. Right heteromorphic valve. Västergötland, Stora Åsbotorp boring, 74.37 m. *Schroeteri* beds. SGU. ×25.
18. Left heteromorphic valve in lateral view. The ornamentation is poorly preserved. Östergötland, Motala boring, 100.05 m. *Crassicauda* limestone. SGU. ×25.

19–20. Left tecnomorphic valve in lateral and ventral view. Öland, Böda Hamn boring, 13.05 m. Lowermost *Crassicauda* limestone. UM no. Öl. 114. ×25.

Euprimites suecicus (THORSLUND, 1940)

21. Holotype. Left heteromorphic valve in lateral view. Jämtland, exposure 1.2 km W of Tandsbyn railway station. *Ludibundus* limestone. SGU. Coll. P. THORSLUND 1934. Figured by THORSLUND 1940, Pl. 2, Fig. 14. ×25.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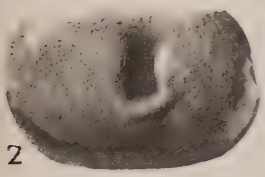
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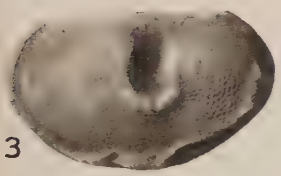
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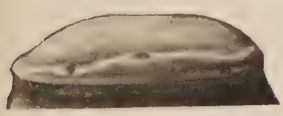
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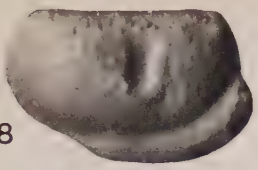
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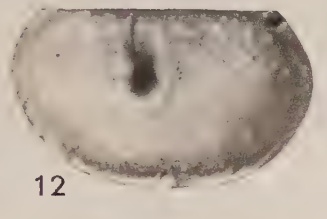
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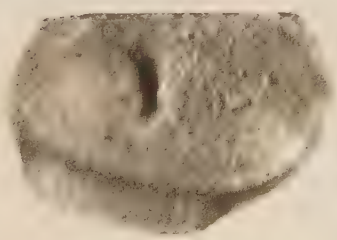
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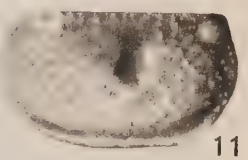
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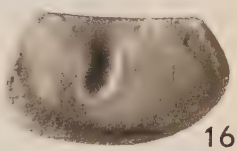
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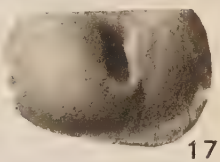
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Plate VIII

All specimens figured have been found in erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone.

Euprimites suecicus (Thorslund, 1940)

All figures magnified × 25.

1–2. Right tecnomorphic valve in lateral and ventral view. Note the distinct velar ridge. UM no. T 118. Coll. P. Thorslund 1928.
3–4. A large tecnomorphic carapace in dorsal and ventral view. UM no. T 116.
5. Right tecnomorphic valve with a long dolon in lateral view. UM no. T 110a.
6. Left heteromorphic valve with a long dolon in lateral view. UM no. T 108. Coll. P. Thorslund 1928.
7–8. Left heteromorphic valve with a dolon of intermediate length in lateral and ventral view. The dolonal flange has been removed in order to expose the subdolonal field. Note the pronounced upward curve of the contact area between the dolon and the domicilium. UM no. T 107.
9. Left heteromorphic valve with a short dolon in lateral view. UM no. T 111. Coll. P. Thorslund 1928.
10–11. A small left tecnomorphic valve in lateral and ventral view. No velar structure is developed. UM no. T 126.

Levisulculus lineatus n. sp.

12. Holotype. Left heteromorphic valve in lateral view. UM no. T 89. × 37.5.
13–14. Left heteromorphic valve in lateral and ventral view. UM no. T 90. × 37.5.
15. Right heteromorphic valve in lateral view. UM no. T 91. × 37.5.

Levisulculus troedssoni (Thorslund, 1940)

16. Lateral view of a rather large left tecnomorphic valve with well-developed tubercles. UM no. T 274. × 50.
17–18. Left tecnomorphic valve in lateral view. Fig. 17 shows the outline, and Fig. 18 (illuminated from behind) the reticulate ornamentation. UM no. T 92. × 40.

Levisulculus granulosus (Thorslund, 1940)

19. Holotype. Right tecnomorphic valve in lateral view. UM no. T 11. × 40. Coll. P. Thorslund 1931. Figured by Thorslund 1940, Pl. 1, Fig. 16.

Plate IX

All figures magnified ×15.

Tallinnella dimorpha Öpik, 1937

1. Left valve in lateral view. Siljan district, Fjäcka, locality No. 3. *Crassicauda* limestone. UM no. D 431.
2–3. Right valve in lateral and ventral view. South Bothnian boulder Bergsbrunna No. 1. Uppermost *Crassicauda* limestone. UM no. B 241.
4. Left valve in lateral view, beneath it the contact margin and the velar flange of the right valve is visible. Siljan district, Fjäcka, locality No. 1. *Crassicauda* limestone. UM no. D 429.
5–7. Right valve in lateral, dorsal, and ventral view. The ventral view is not taken in strictly ventral, but in somewhat ventrolateral direction. Locality and horizon as in Figs. 2–3. UM no. B 242.
8. Right valve in lateral view. Siljan district, Furudal, quarry at the Kalkbergsbäcken. *Crassicauda* limestone. Coll. V. Jaanusson, J. Martna, and H. Neuhaus 1945. UM no. D 430.
9. Anterior part of a right valve in lateral view. Siljan district, Fjäcka, locality No. 7. Lowermost *Ludibundus* limestone, ca. 17.5–18.0 m below the lower boundary of the bentonite beds. UM no. D 428.

Tallinnella cf. *angustata* (Krause, 1891)

10. Left valve in lateral view. Öland, Gammalsby bore, at the level of 6.30 m. *Schroeteri* limestone. SGU.

Tallinnella cf. *lata* (Krause, 1891)

11. Right valve in lateral view. Öland, Folkeslunda sjöbodar. Gray *Schroeteri* limestone. RM no. Ar. 19811. Coll. J. G. Andersson, 1892.

Tallinnella sebyensis n. sp.

12–13. Holotype. Left valve in lateral and ventral view. Öland, Seby. Uppermost *Schroeteri* limestone. UM no. Öl. 129.

Tallinnella tumida Henningsmoen, 1953

Both specimens figured have been found by N. Spjeldnæs in the section Bjerkås-Djuptrekkodden, Røyken, Oslo Region. $4a\alpha_3$.

14. Left valve in lateral view. OM.
15. Holotype. Left valve in lateral view. The peripheral margin of the posteroventral part of the velar structure is broken off. OM no. 66421. Figured by Henningsmoen 1953b, Pl. 2, Fig. 3.

Tallinnella pachydactyla n. sp.

16–17. Holotype. Right valve in ventral and lateral view. The subvelar field is not exposed. Öland, Skärlöv bore, 3.35 m. Lowermost *Schroeteri* limestone. SGU.

Tallinnella trident Henningsmoen, 1953

18. Cast of the external imprint of the holotype. The area adjacent to the dorsal margin of the valve incomplete. Oslo region, Muggerudkliva, Sandsvær. $4a\alpha_2$. OM no. 66420. The external imprint has been figured by Henningsmoen 1953b, Pl. 2, Fig. 1.

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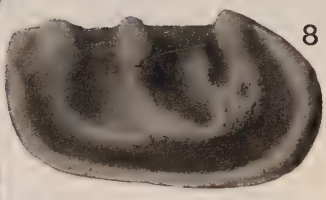
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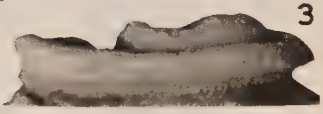
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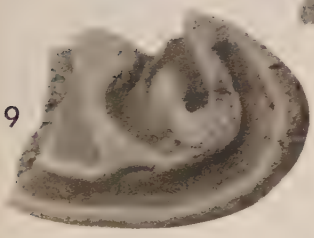
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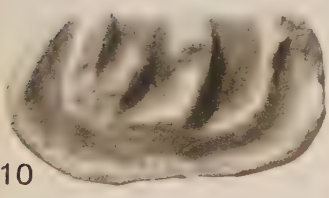
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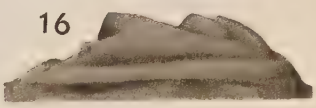
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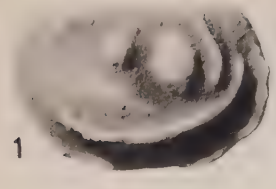
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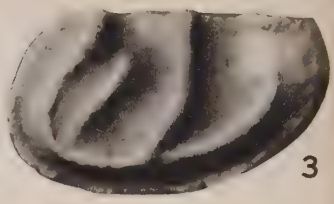
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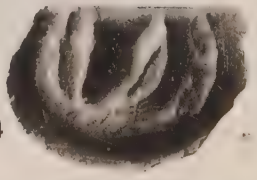
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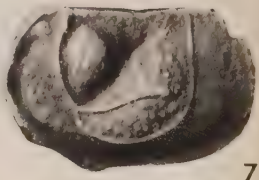
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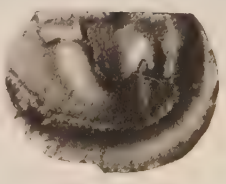
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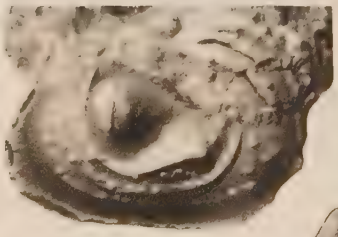
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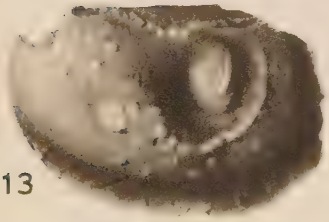
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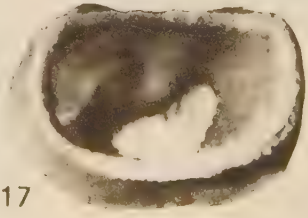
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Plate X

Lennukella europaea (Öpik, 1937)

1. Right valve in lateral view. South Bothnian erratic boulder Bergsbrunna No. 1. Uppermost *Crassicauda* limestone. UM no. B 243. ×20.

Tallinnellina n. sp.

2. Lateral view of a left valve with a convex velar flange (heteromorph?). Oslo region, Ringsaker, Heramb. Zone of *Megistaspis estonica*. OM no. 66390. Coll. S. Skjeseth 1949. ×25. Figured as *Tallinnella primaria* (Öpik) by Henningsmoen 1954a, Pl. 1, Fig. 4.

Tallinnella? bohemica (Barrande, 1872)

3. Cast of an external imprint of the left valve. Bohemia, Trubin. RM no. Ar. 39169. ×15.

Tallinnellina lanceolata (Hessland, 1949)

4. Holotype. Left valve with a concave velum (tecnomorph?) in lateral view. Siljan district, Stenberg. *Expansus* limestone. UM no. ar. os. 660. Coll. I. Hessland. ×35. Figured by Hessland 1949, Pl. IX, Figs. 10a, 10b.

Rigidella mitis (Öpik, 1935)

5. Lateral view of a right valve with an anteroventrally convex velum. Probably a heteromorph. Estonia, Tallinn. *Lepidurus* limestone ($B_{II}\gamma$). UM no. E 6. ×35.

Steusloffia linnarssoni (Krause, 1889)

6. Left valve in lateral view. Öland, Gammalsby boring, at the level of 8.20 m. Lowermost *Crassicauda* limestone. SGU. ×15.
7. Left valve in lateral view. Västergötland, Kinnekulle, Norra Skagen boring, 23.39 m. *Crassicauda* limestone. SGU. ×15.
8–9. Left valve of a carapace in lateral view and the whole carapace in dorsal view. South Bothnian area, erratic boulder Erken No. 10. *Crassicauda* limestone. UM no. B 302.
10. Left valve in lateral view. Öland, Gammalsby boring, 0.60 m. *Crassicauda* limestone. SGU. ×15.

Steusloffia multimarginata Öpik, 1937

11. Right valve in lateral view. Siljan district, Fjäcka, locality No. 7, sample No. D 90. Lowermost *Ludibundus* limestone. UM no. D 424. ×15.
12. Fragmentary left valve in lateral view. Note the distinct row of tubercles ventrally of the ventral part of C 4. Erratic boulder from the Tvären area, Södermanland. Lowermost *Ludibundus* limestone. UM no. T 77. ×15. Coll. P. Thorslund 1931.
13. Lateral view of a young right valve with incompletely developed crests. Locality and horizon as in Fig. 12. UM no. T 23. ×25. Coll. P. Thorslund 1928. Figured as *Steusloffia costata* (Linrs.) by Thorslund 1940, Pl. 3, Fig. 3.
14. Lateral view of a young right valve with incompletely developed crests. Locality and horizon as in Fig. 12. UM no. T 76. ×25.

Steusloffia costata (Linnarsson, 1869)

15. Right valve in lateral view. Siljan district, Fjäcka. *Ludibundus* limestone. UM no. D 422. ×15. Coll. P. Thorslund 1930.
16–17. Ventral and internal view of a young right valve with a simple ventral margin of the velar flange. Västergötland, Kinnekulle, Kullatorp boring, 71.03 m. *Ludibundus* beds. UM no. Vg. 79. ×20. Coll. P. Thorslund.
18. Left valve in lateral view. Locality and horizon as in Figs. 16–17. UM no. Vg. 78. ×15. Coll. P. Thorslund. The ventral view of the same specimen is given on Pl. XI, Fig. 1.

Plate XI

Steusloffia costata (Linnarsson, 1869)

1. Left valve in ventral view. Note the double ventral margin of the velar flange. UM no. Vg. 78
×20. The lateral view of the same specimen is given on Pl. X, Fig. 18.

Sigmoopsis bergsbrunnae n. sp.

All specimens magnified ×25.

2. Right tecnomorphic valve in lateral view. South Bothnian erratic boulder Bergsbrunna No. 1.
Uppermost *Crassicauda* limestone. UM no. B 283.
3. Left heteromorphic valve in lateral view. South Bothnian erratic boulder Erken No. 10. *Crassi*
cauda limestone. UM no. B 297.
4. Right heteromorphic valve in lateral view. Locality and horizon as in Fig. 2. UM no. B 28
5. Holotype. Right heterom. valve in lateral view. Locality and horizon as in Fig. 2. UM no. B 28
6. Right heteromorphic valve in lateral view. Kinnekulle, Norra Skagen boring, 25.73 m. SGU

Sigmoopsis platyceras (Öpik, 1937)

Siljan district, Fjäcka, locality No. 8. *Ludibundus* limestone, about 11.5 m below the lower boundary c
the bentonite beds. Magnification ×25.

7. Left tecnomorphic valve in lateral view. UM no. D 541.
8. Left tecnomorphic valve in lateral view. UM no. D 542.

Sigmoopsis sp. A

9. Right tecnomorphic valve in lateral view. Erratic boulder of the Tvären area, Södermanlan
Lowermost *Ludibundus* limestone. UM no. T 31. ×25. Coll. P. Thorslund 1928. Figured
Ceratopsis obliquejugata (Fr. Schm.) by Thorslund 1940, Pl. 3, Fig. 13.

Sigmoopsis sp. B

10. Left heteromorphic valve in lateral view. Västergötland, Billingen, Stora Åsbotorp bore, 57.85 r
Crassicauda beds. SGU. ×25.

Polyceratella bonnemai (Thorslund, 1940)

11–12. Holotype. Right tecnomorphic valve in lateral and ventral view. Note the fairly broad velar flang
The subvelar field is not exposed. Erratic boulder of the Tvären area. Lowermost *Ludibundus* lim
stone. UM no. T 36. ×25. Coll. P. Thorslund 1931. Figured by Thorslund 1940, Pl. 4, Fig. 1

Polyceratella kuckersiana (Bonnema, 1909)

13–14. Left heteromorphic valve in lateral view. Fig. 14 is a photograph of the specimen immersed
alcohol in order to show the width of the histial (dolonal) flange (visible on this Fig. as a da
border around the non-dorsal part of the lateral surface of the domicilium). Öland, exposure
the beach of Böda Hamn. *Ludibundus* limestone. UM no. Öl. 826. ×25.
15. Right tecnomorphic valve in lateral view. Estonia, Kukruse. $C_{II}\alpha$. UM no. E 15. ×37.5.

Sigmobolbina sigmoidea n. sp.

16–18. Holotype. Left heteromorphic valve in lateral and ventral view. Fig. 17 is a photograph of t
specimen immersed in alcohol in order to show the width of the histial (dolonal) flange (visib
on this Fig. as a dark border surrounding the lateral surface of the domicilium ventrally a
anteroventrally). Öland, Gammalsby bore, 1.40 m. *Crassicauda* limestone. SGU. ×25.
19. Right heteromorphic valve in lateral view. Ibid., 3.45 m. *Crassicauda* limestone. SGU.
20. Left tecnomorphic valve in lateral view. Ibid., 3.10 m. *Crassicauda* limestone. SGU.

Sigmobolbina variolaris (Bonnema, 1909)

21. Right heteromorphic valve in lateral view. Erratic boulder of the Tvären area. Lowermost *Ludibund*
limestone. UM no. T 34. ×37.5. Coll. P. Thorslund 1931. Thorslund 1940, Pl. 3, Fig. 16.

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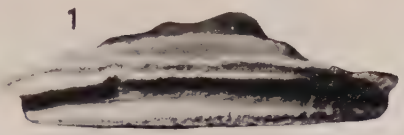
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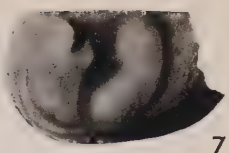
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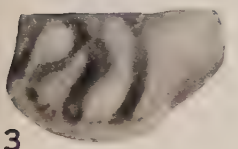
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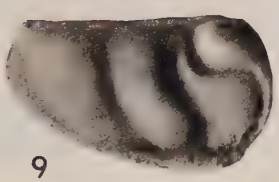
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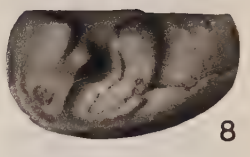
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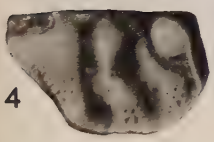
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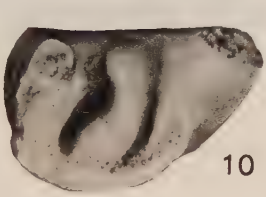
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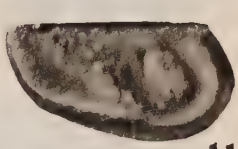
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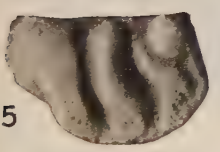
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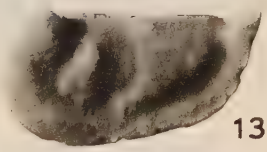
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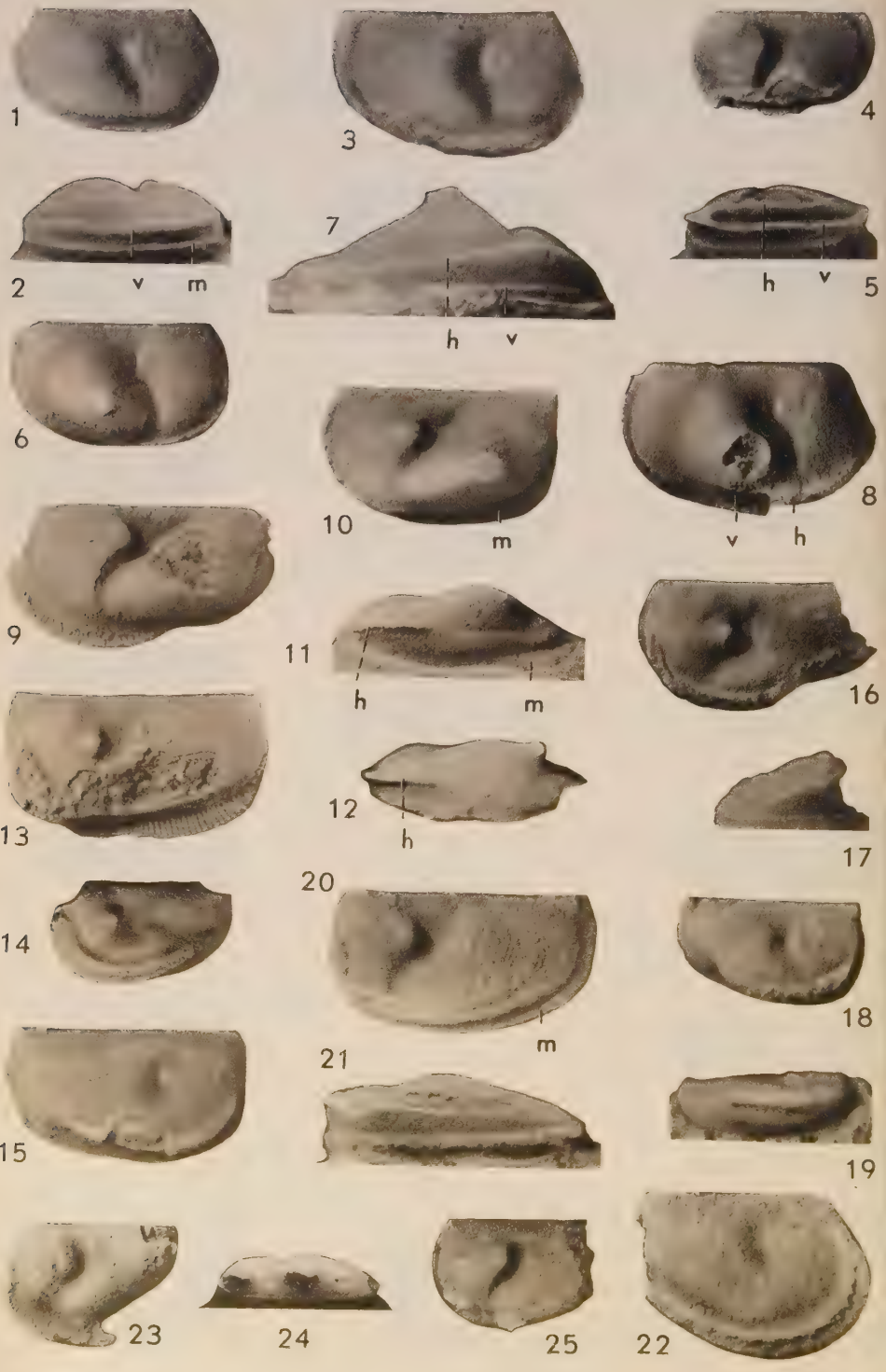
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Plate XII

Sigmobolbina pentagona n. sp.

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone.

1–2. Right tecnomorphic valve in lateral and ventral view. m = marginal ridge; v = velar ridge. UM no. T 146. × 37.5.

3. Holotype. Right heteromorphic valve in lateral view. UM no. T 145. × 37.5.

4–5. Left heteromorphic valve in lateral and ventral view. The dolonal flange has been removed in order to expose the subdolonal field. h = contact area between the dolon and the domicilium; v = velar flange, its peripheral margin broken off; below it the subvelar field is visible. Note the coalescence of the histial and velar structures on the right. UM no. T 144. × 25.

Lomatobolbina mammillata (Thorslund, 1940)

Both specimens figured have been found by P. Thorslund 1935 in an exposure 1.2 km W of Tandsbyn railway station, Lockne area, Jämtland. *Ludibundus* limestone.

6–7. Right tecnomorphic valve in lateral (× 25) and ventral (× 37.5) view. The top of the spine on the posteroventral lobe is broken off. h = histial ridge; v = velar ridge. SGU.

8. Right heteromorphic valve in lateral view. The spine on the posteroventral lobe and the posterior part of the histial dolon are broken off. Beneath the broken part of the histial dolon the velar flange (v) is visible. h = histial flange (dolon); v = velar flange. SGU. × 25.

Lomatobolbina craspedota n. sp.

Erratic boulders of the Tvären area. Lowermost *Ludibundus* limestone. Magnification × 37.5.

9. Holotype. Left heteromorphic valve in lateroventral view. Note the broad and radially striated dolonal flange. UM no. T 148.

10–11. Left tecnomorphic valve in lateral and ventral view. The spine on the posteroventral lobe is broken off. Note the distinct histial ridge (h) and the broad marginal flange (m). UM no. T 147.

12. Left tecnomorphic valve in ventral view. The marginal flange and the top of the spine on the posteroventral lobe are broken off. Note the distinct histial ridge (h). UM no. T 149.

Oecematobolbina nitens n. sp.

Erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone.

13. Left heteromorphic valve in lateral view. The posterior part of the histial structure has been removed in order to expose the striated marginal flange. UM no. T 155. × 37.5.

14. Holotype. Left heteromorphic valve in lateral view. In order to get a clear picture of the histial dolon the specimen has been illuminated from the ventral direction. UM no. T 267. × 25.

15. Right tecnomorphic valve in lateral view. The marginal flange is not visible. UM no. T 266. × 40.

16–17. Left tecnomorphic valve in lateral and anterior view. UM no. T 152. × 37.5.

18–19. Right tecnomorphic valve in lateral and lateroventral view. UM no. T 153. × 37.5.

Oecematobolbina sp. A

20–21. Left tecnomorphic valve in lateral and ventral view. Note the two distinct rows of oblong pits upon the histial structure. m = marginal flange. Erratic boulder of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone. UM no. T 151. × 37.5.

Oecematobolbina sp.

22. Lateral view of a right heteromorphic valve. The posterior part of the valve is broken off. Västergötland, Kinnekulle, Norra Skagen boring, 7.95 m. SGU. × 25. Cf. also Text-fig. 44.

Grammolomatella vestrogothica (Henningsmoen, 1948)

23. Holotype. Left heteromorphic valve in lateral view. Västergötland, Kinnekulle, Kullatorp boring, 57.00 m. Green *Tretaspis* mudstone. Coll. G. Henningsmoen. UM no. Vg. 62. × 25. Figured by Henningsmoen 1948, Pl. XXV, Fig. 12.

24–25. Left tecnom. valve in ventral and lateral view. The terminations of the histial spines are broken off. Ibid., 57.75 m. Green *Tretaspis* mudstone. Coll. G. Henningsmoen. UM no. Vg. 89. × 25.

Plate XIII

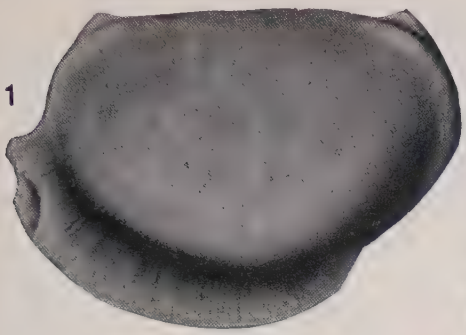
Oepikella tvaerensis THORSLUND, 1940

All specimens figured have been found in erratic boulders of the Tvären area, Södermanland. Lowermost *Ludibundus* limestone.

1–5. A large left heteromorphic valve in lateral, posterior, dorsal, and ventral view. × 15. Fig. 5 gives the ventral, peripheral part of the frill of the same specimen photographed with a thin coating of shellac in order to show the internal partitions of the frill. × 50. UM no. T 4. Coll. P. THORSLUND 1931. Figured as *Öpikella asklundi* by THORSLUND 1940, Pl. 1, Fig. 5.

6–9. A small right heteromorphic valve in dorsal, posterior, ventral, and lateral view. UM no. T 2. × 15. Coll. P. THORSLUND 1931. Holotype of *Öpikella asklundi* THORSLUND, 1940, Pl. 1, Fig. 3.

10–13. A large left tecnomorphic valve in lateral, dorsal, anterior, and ventral view. Note the curved row of pits which forms the ventral margin of the pitted area of the valve. UM no. T 195. × 15.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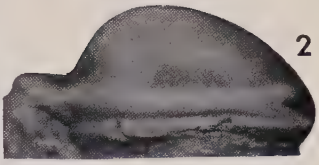
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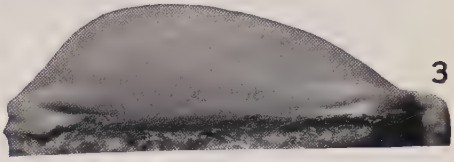
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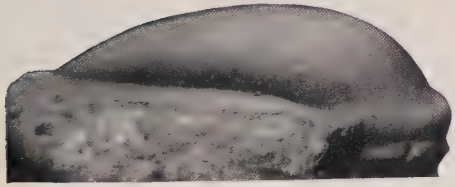
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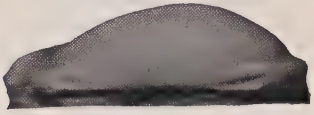
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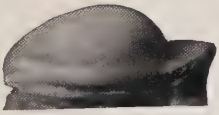
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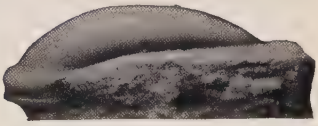
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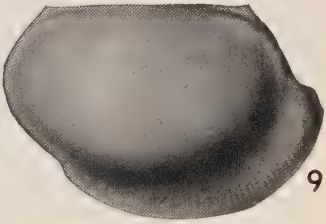
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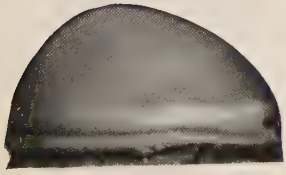
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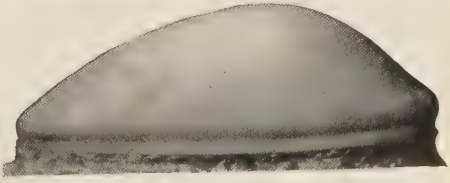
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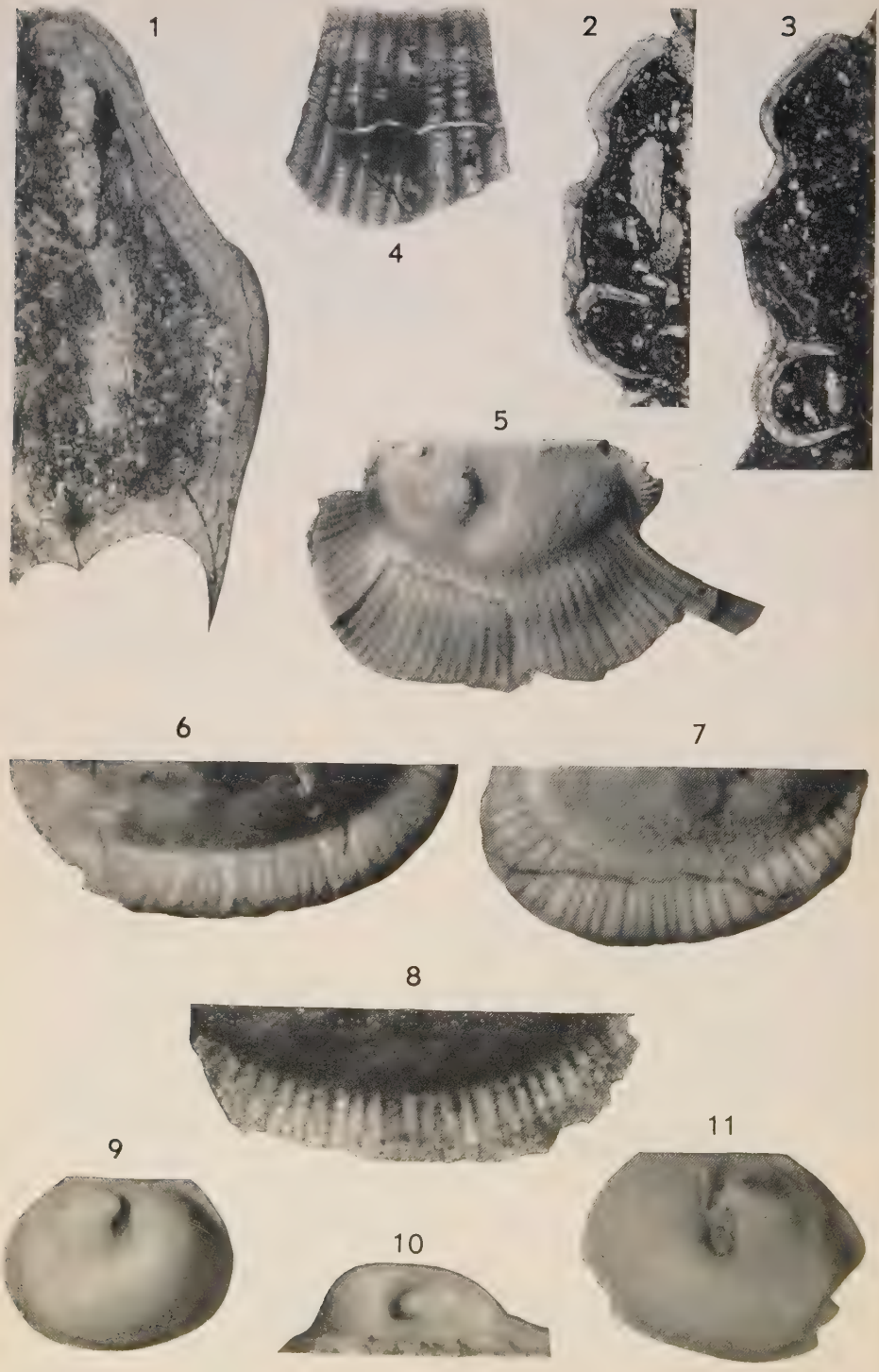
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Plate XIV

Euprimites effusus n. sp.

1. Transverse thin section of a heteromorphic valve, cf. Text-figs. 5B and 29A. Öland, Böda Hamn boring, at the level of 20.72 m. ×60.

Uhakiella periacantha n. sp.

2. Transverse thin section of a heteromorphic valve, cf. Text-fig. 25. South Bothnian area, erratic boulder Bergsbrunna No. 1. ×60.

Laccochilina (Laccochilina) paucigranosa n. sp.

3. Transverse thin section of a heteromorphic valve, cf. Text-fig. 11C. South Bothnian area, erratic boulder Erken No. 10. ×60.

Oepikium sp. A

4–5. Left tecnomorphic valve. 4, part of the frill in transmitted light, ×30. 5, lateral view of the valve, ×15. The peripheral part of the frill is broken off along the ventral margin. South Bothnian area, erratic boulder Erken No. 10. *Crassicauda* limestone. UM no. B 303.

Laccochilina (Prochilina) decumana (Bonnema, 1909)

6. Dolonal frill immersed in alcohol; lateral view showing the partitions within the frill ×25. Tvären area, Ringsö, boulder of the *Ludibundus* limestone. Coll. P. Thorslund 1928. UM no. T 265.

Platybolbina kapteyni (Bonnema, 1909)

7. Dolonal frill immersed in alcohol; lateral view showing the partitions within the frill. ×40. Tvären area, Ringsö, boulder of the *Ludibundus* limestone. UM no. T 275.

Actinochilina cf. *suecica* (Thorslund, 1948)

8. Tecnomorphic frill immersed in alcohol; lateral view showing the partitions within the frill. ×50. LM. The same specimen is figured as Fig. 10 on Pl. III.

Craspedopyxion undulosum (Öpik, 1937)

9–10. Right valve in lateral and dorsal view. ×40. Estonia, Kukruse Stage (probably $C_{II}\alpha$). UM no. E 17.

11. Left valve in lateral view. ×40. Locality and horizon as in Figs. 9–10. UM no. E 16.

Plate XV

Conchoprimitia leperditioidea THORSLUND, 1940

1–3. Right valve with a well-preserved surface in lateral, ventral, and dorsal view. Siljan district, Fjäcka, locality No. 7. Lower part of the *Ludibundus* limestone. UM no. D 544. ×20.

4–6. Carapace of the elongate type; right valve in lateral, carapace in dorsal and ventral view. Öland, Böda Hamn boring, at the level of 0.98 m. *Ludibundus* limestone. UM no. Öl. 831. ×20.

Conchoprimitia? conchoidea (HADDING, 1913)

All specimens figured have been found by A. HADDING in the exposure No. III: 6 of Röstånga, Scania. *Nemagraptus gracilis* shale. Magnification ×25.

7. Lectotype. Left valve with a valve of the preceding instar still attached and with a groove upon the latter valve obviously due to the pressure of the free margin of a still earlier instar. LM no. 2513 t. Figured by HADDING 1913, Pl. VI, Fig. 15.

8. Both valves of a carapace in juxtaposition. LM no. 2509 t. Figured by HADDING 1913, Pl. VI, Fig. 11.

9–11. A small right valve in lateral, ventral, and dorsal view. Carinal bend poorly developed. From the same slab of shale as the specimen figured by HADDING on Pl. VI, Fig. 10. LM.

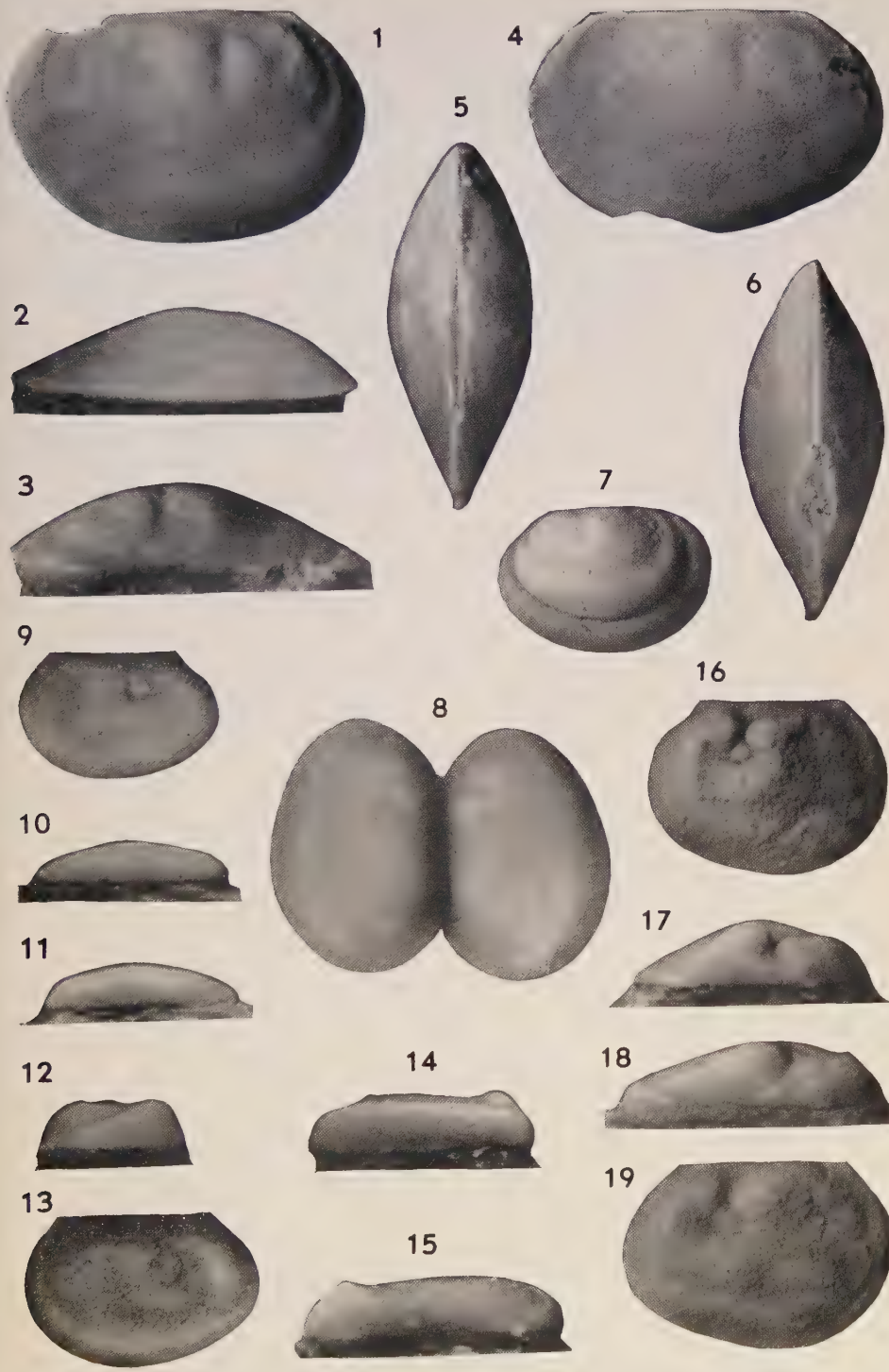
Pyxion carinatum (HADDING, 1913)

12–15. Lectotype. Right valve in anterior, lateral, ventral, and dorsal view. Scania, Röstånga, locality No. III: 13. *Nemagraptus gracilis* shale. LM no. 2510 T. 12–14, ×25; 15, ×30. Figured by HADDING 1913, Pl. VI, Fig. 12, and THORSLUND 1948, Pl. XX, Fig. 2.

Parapyxion subovatum (THORSLUND, 1948)

16–17. Left valve in lateral and dorsal view. Västergötland, Kinnekulle, Kullatorp boring, 76.84 m. *Ludibundus* mudstone. Coll. P. THORSLUND. UM no. Vg. 713. ×30.

18–19. Holotype. Left valve in dorsal and lateral view. Västergötland, Kinnekulle, Kullatorp boring, 77.42 m. *Ludibundus* mudstone. Coll. P. THORSLUND. UM no. Vg. 17. ×30. Figured by THORSLUND 1948, Pl. XX, Fig. 5.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The Students' Association of Natural Science, Uppsala
Geological Division

(Geologiska sektionen av Naturvetenskapliga studentsällskapet i Uppsala)

Meeting November 10, 1956.

14 persons present.

Lecture by Mr. ROBERT VON ENZMANN: "Orbicular rocks of the Kheis geosynclinal system, Namaqualand, South Africa."

Meeting November 29, 1956.

13 persons present.

Lecture by Professor ASTRID CLEVE VON EULER: "Sandarna, age and settlement."

Meeting December 18, 1956.

16 persons present.

Lecture by Dr. BERTIL DAHLMAN: "The uraniferous alum shale of Sweden."

Meeting March 8, 1957.

24 persons present.

Lecture and demonstration by Mr. ERIC STÅHL: "Sampling and preparation of glacial clays in plastics."

Lecture by Mr. BUSTER SUND: "Joints and ground water in solid rocks."

Meeting March 29, 1957.

21 persons present.

Lecture by Dr. ERIK ERIKSSON: "Geochemical aspects of the circulation of marine salt in nature."

Meeting April 12, 1957.

19 persons present.

Lecture by Dr. BROR WIDELAND: "Determinations of gravitation."

Meeting April 26, 1957.

28 persons present.

Lecture by Dr. K. GÖSTA ERIKSSON: "Recent research on the postglacial climate of India and the Mediterranean countries."

Bulletin of the Geological Institutions

OF

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EDITORS

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Contents of Parts 3–4

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